EPIDEMIC, PRIMARY VIRUS INFECTIONS OF THE CENTRAL NERVOUS SYSTEM OF MAN

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CLASSIFICATION

IN the fourth lecture on the Kober Foundation delivered early in 1928 at Georgetown University, Dr. Simon Flexner, in describing the epidemic diseases of the central nervous system of man prevailing in different areas of the world in the first quarter of the twentieth century, mentioned only one having a proved virus origin, namely, poliomyelitis. He described another malady, occurring during the latter third of this period, then called "sleeping sickness" (epidemic encephalitis; encephalitis lethargica or von Economo's disease, later, encephalitis Type A), but its causal agent could only be surmised as a virus; indeed, its cause is still, to-day, undetermined. Dr. Flexner went on to emphasize that the latter type of encephalitis, or brain inflammation, should not be confused with the malady that complicates the virus diseases, chiefly of childhood, such as measles and mumps, and is sometimes a sequel of anti-smallpox vaccination and of other virus infections, such as influenza. Localized epidemics of Australian "X" encephalitis arose in 1917–1918, continuing to 1926; the disease was found to be caused by a virus—first thought to be poliomyelitis, then Japanese B or louping-ill virus soon to be described. Since this virus was lost it has, therefore, not as yet been classified. Thus, in the first quarter of the present century, the world was confronted by epidemics of two plagues of proved virus origin which attacked the cen-

tral nervous system of man, poliomyelitis and Australian
"X" disease.[1]   To be sure, epidemics of encephalitis, as
distinct from poliomyelitis, arose now and then before
this period, but the causal factor of the diseases was con-
sidered as unknown or as the result of organic involve-
ment of the brain.

What happened in the 15 years since 1930 is truly
amazing and the cause of the phenomenon is still to be
conjectured. For in that decade and a half a large num-
ber of epidemics in man, of distinct, primary virus in-
fection of the central nervous system, has been reported
from various parts of the globe. They are given in
chronological order (the dates refer to the year of the
first epidemic or the first isolation of the virus: when
two dates are mentioned, the second refers to virus isola-
tion): Western equine encephalomyelitis (inflammation
of the brain and the spinal cord), (1930); the Eastern
type (1933); St. Louis encephalitis (1933); Japanese B
encephalitis (1924; 1934); Russian tick-borne or spring-
summer encephalitis (1937); Venezuelan equine enceph-
alomyelitis (1938); and acute hemorrhagic meningo-
encephalitis (1944). In addition, the field workers of
the Rockefeller Foundation, in searching for yellow fever
suspects in Africa, recently encountered three "new"
viruses—whether they are potentially "encephalitis"
viruses still remains to be seen. They are the West Nile
(1940) recovered from the blood of a native Uganda
woman having fever; the Bwamba fever (1941), isolated
from the blood of nine natives having, generally, fever,
headache and backache, and the Semliki Forest (1944)
virus, obtained from infected local mosquitoes; many
natives, however, showed specific antibody in the blood
serum neutralizing this virus, thus indicating a prior

[1] Later in 1928, Dr. T. M. Rivers, in a general review of viruses published
in the book under his editorship, *Filterable Viruses*, lists as types of en-
cephalitis then known: (1) lethargic; (2) following vaccination; (3) Japa-
nese 1924; (4) Koritschoner, and (5) Australian "X." The causal agent
of No. 3, epidemics of which were localized in Japan, was definitely found
to be an independent virus a decade later; No. 4 went into oblivion with
time as a strain of rabies, and No. 5 survived as a ghost.

infection. The presence of these specific antibodies in many natives lends significance to all three of the latter infective agents. Finally, there are in this and other lands, including the United States, a number of cases of encephalitis, suspiciously like the infectious type, for which no definite causal agent has been revealed.

Apart from the various kinds of epidemic primary virus encephalitis already mentioned, one can add another group of those that are sporadic, *i.e.*, non-epidemic (the dates refer to the year of virus isolation) : lymphocytic choriomeningitis (1934) and its pseudo form (1939), a variant, and louping-ill (1931), a disease of sheep, generally of Scotland, which has attacked certain laboratory workers during the course of investigations on the virus, and now (1945) reported to attack sheep and man in White Russia. To make the list still more complete, there should be added the encephalitides and the viruses attacking nerve tissue (neurotropes) of lower animals which convey the infection to man by bite or inoculation : rabies (Pasteur, 1881, added even though it has an old history) and Sabin's B virus of monkeys (1934) and finally, the maladies which can be induced by familiar viruses ordinarily not producing clinically apparent reactions in the central nervous system. Isolated fatal cases of encephalitis have been reported in the last decade caused by the viruses such as those of simple herpes (wind-blister), of lymphogranuloma venereum (climatic bubo), and of mumps.

Although the present article concerns itself with epidemic primary virus encephalitis of man, it should be noted that a number of similar types of disease have been disclosed, within the same recent period, among lower animals. Thus, before 1930, the known veterinary primary virus encephalitides comprised rabies, Borna's disease in various species (also the Moussu-Marchand type in the horse) ; guinea pig and hen paralysis; epizootic fox encephalitis and pseudorabies.[2] With these, were recog-

[2] In 1931, Shope demonstrated that the virus of a disease present in cattle in the United States and known as ''mad itch'' was identical with that of pseudorabies (Aujeszky's disease).

nized the secondary infections of the central nervous system accompanying other visceral virus maladies such as distemper of dogs, swine fever, fowl plague, and others. After 1930 a number of epidemic primary virus encephalitides, apart from the three types of equine encephalomyelitis already mentioned, were brought into the light: louping-ill of sheep (1930); encephalomyelitis of swine or Teschen disease (1933); Theiler's virus disease (spontaneous encephalomyelitis; poliomyelitis) of mice (1934); avian encephalomyelitis (epidemic tremor) (1934); infection of mice with lymphocytic choriomeningitis virus (1935); canine encephalitis (1940) and avian pneumo-encephalitis (a "respiratory-nervous disorder" of chickens) (1941).

SUMMARY OF CERTAIN FEATURES OF THE EPIDEMIC VIRUS INFECTIONS OF THE CENTRAL NERVOUS SYSTEM OF MAN

Of this group of scourges, the one which has been recorded from the earliest times, even, as some would believe, in prehistoric ages, is poliomyelitis or infantile paralysis. It differs essentially from the encephalitides to be mentioned in that it is not primarily an inflammation of the brain, although the latter organ is usually involved, but one of the anterior horns, the gray matter, of the spinal cord. Destruction of the motor nerve cells of this area leads to the flaccid paralysis which ordinarily develops rapidly during the course of infection. In modern times, the earliest epidemics suspected as being of poliomyelitis have been disclosed as occurring in England in 1835 and in the United States, in Louisiana, in 1841. The first systematic description of the disease was published in 1840, based on an epidemic in Sweden. Recent studies point to the fact that there are many types of poliomyelitis viruses. Thus far five types have been revealed: a common one which is highly specific for man, not being transmissible in series to lower animals; the second, also common, occurs in man but can be transmitted to monkeys; a third, rarer, to which certain rodents

such as albino mice and cotton rats are also susceptible
to artificial inoculation; a fourth, the highly specific type
of poliomyelitis of mice (spontaneous Theiler's disease)
and the fifth, poliomyelitis of swine (Teschen disease),
also specific only for that species. In addition there are
different strains of some of these types.

The epidemic encephalitides of virus origin occurring
in man are affections in which the brain is primarily
involved and, in such as are encephalomyelitic in nature,
the spinal cord is inflamed primarily, or by extension
of the cerebral process. The signs and symptoms of an
infection will depend on the area of the central nervous
system involved in any particular patient, be it the
meninges or the cortical or basal (ganglia) area of the
brain, or the spinal cord. While there may be a char-
acteristic clinical picture to demarcate an epidemic type,
any one individual case by itself offers great difficulty
for the diagnosis of the special form of disease from the
clinical picture alone. As a rule, the laboratory is called
upon, especially at the beginning of an epidemic, to assist
in the differentiation of the prevailing epidemic disease.

While poliomyelitis virus is present over the entire
world, the clinically apparent disease is more commonly
observed in the temperate zone, for example, in the
United States and Canada, Scandinavia, New Zealand
and Australia. The epidemic virus encephalitides arise
generally in definite parts of the globe, each form, as it
were, attacking within its specified boundaries. Thus,
at the present time, in the New World, the Eastern type
of equine encephalomyelitis as it occurs in man and in
horses is found, as a rule, in the Eastern states of the
United States and in Ontario, Mexico, Panama, Cuba and
Brazil; the Western, in the Western states, Canada and
Argentina; and the Venezuelan, in Trinidad, Colombia,
Ecuador and Venezuela. In fact, only three states of the
United States, Alabama, Michigan and Texas, harbor
cases of both Eastern and Western types. For the
human infection, St. Louis encephalitis prevails chiefly in
the Middle and Western states; Japanese B type in the

Far East and certain neighboring Pacific Islands; Russian tick-borne encephalitis in the Far East and (recently) in the European part of the Soviet Union, while louping-ill occurs in White Russia. Acute primary hemorrhagic meningoencephalitis has been reported thus far only in Russia.

Most of the maladies just described have been shown to be transmitted from animal to animal and from animal to man by mosquitoes, ticks, and possibly mites; hence they are designated as arthropod-borne virus encephalitides. Specifically, the vector (transmitter) of Western and St. Louis encephalitis is *Culex tarsalis* mosquitoes and the reservoir (source) of the virus is in woodland animals, especially birds, and of the latter, as shown by Hammon, particularly apparently healthy but infected barnyard fowl. Recently it has been shown that mites convey the infection from chicken to chicken which are not thereby made sick, but in this manner the virus is propagated and spread about. For the Russian tick-borne virus the tick, *Ixodes persulcatus,* is the vector and woodland or forest animals the reservoirs. It has been said that man is only a casual victim of the bite of an "animal" tick harboring an "animal" virus. For the other epidemic virus encephalitides, the reservoirs are still to be definitely established; on the other hand, the mosquito is suspected, but the species not as yet identified, as being the vector of Japanese B, and Eastern and Venezuelan types of infection. However this is, these plagues are prevalent during the warmest months of the year, at the time when insects swarm. Human poliomyelitis, as distinct from the encephalitides, is also a summer disease but winter epidemics do occur; flies have been implicated as vectors. Even were flies involved in some epidemics, they can not be held responsible for others; furthermore, not all epidemics follow the pattern of those that are fly-borne.

The tissue changes induced by the virus of the latter disease are characteristic in that there is primarily de-

struction of the nerve cells (neurons) in the anterior horn—the gray matter—of the spinal cord which predominates the other lesions. These, chiefly, are degeneration of the nerve cells, cellular infiltration about the blood vessels, varying degrees of hemorrhage, cellular invasion into the site of the destroyed nerve cell with removal of its remnants—a process termed neuronophagia—and glial cell (framework cell) accumulations. The picture in general is distinct from that found in the epidemic virus encephalitides which show the main seat of attack in the brain and often secondary or no changes in the spinal cord. The reaction, as in poliomyelitis plus changes in the vessel walls, varies in each form of encephalitis in that one or another kind of lesion is more prominent, but for any one case it is impossible to say, as a rule, from pathological examination of the tissues, what was the encephalitic disease that brought about the observed changes.

THE APPARENT INCREASE IN VIRUS ENCEPHALITIS EPIDEMICS IN RECENT TIMES

We now come to an interesting point, namely, the apparent increase throughout a great part of the world of epidemic virus encephalitis disclosed during the past 15 years. It is not proposed to discuss whether these are "new" diseases or not, although records show the prevalence of similar disorders in the past. The identity of the previous epidemics is, however, obscured by the fact that the same methodology on which the present classification is based was, of course, not then available. On the other hand, new forms of old scourges or new types of disease can arise, as is postulated by Theobald Smith and others, just as other maladies, such as sweating sickness in Europe during the end of the fifteenth century, trench fever during the World War I, and, possibly, encephalitis lethargica of that period, can disappear.

The number of encephalitides revealed in the recent short time may be owing, at least in part, to new meth-

ods for isolation of their viruses and their identification. To the important work of Theiler, in 1930, may be ascribed one stimulus for the revelation. He injected directly into the brain of laboratory mice yellow fever virus—then not too well established—in an effort to find out the nature of the causal factor of the disease. His success with such a simple method, in an easily available animal, not only led the way to discoveries of many viruses but also to the preparation of the useful yellow fever vaccine.[3]

Apart from animal inoculation for the isolation of a virus which can then be identified, there are two other laboratory methods devised for this identification, namely, the virus-neutralization and the complement-fixation test. Both depend on the fact that antibody against the virus develops after infection, which is highly specific, *i.e.*, a positive reaction results only between the virus and its own antibody, not any other and vice versa. The antibodies are found in the blood serum, hence they are called "serological." A third test of value for identification of viruses is the resistance or immunity test in immune animals, *i.e.*, animals immunized artificially with a virus, or recovering from an infection with it, are rendered immune on inoculation only of that particular virus, not of any other.

Finally, the response of various animals to experimental inoculation of a virus in question offers a biological test for differentiation, *e.g.*, Japanese B, but not St. Louis encephalitis virus is disease-producing in sheep.

With these tools then the harvest was brought in. On the surface it would appear that the recent encephalitides are merely variants of the lost encephalitis lethargica of 1916–1926: with more precise methods it was broken down to its components. This is, however, not likely since the lethargic disease was a "winter" not a "sum-

[3] Theiler declares his debt to Andervont, who in 1929 used herpes virus in the same way in mice to study the properties of the virus by various routes of inoculation.

mer'' one and no virus could be identified with it as its cause, although the latter group yields up its respective virus with but little effort.

Theoretical Concepts of the Geographical Limitation of the Epidemic Virus Encephalitides

It is tempting to speculate on the relations of the primary epidemic encephalitis viruses of one to another. Casals has shown the close serological relationship between Russian spring-summer, or tick-borne, virus to that of louping-ill, and the serological overlapping of reactions of West Nile, Japanese B and St. Louis encephalitis viruses is well known. Several other investigators have observed cross-complement-fixation among the different viruses of this group with serum of laboratory animals immunized against them. Now, there are many other points of similarity: most of the viruses have their particle diameters at about 25 millimicrons; the pathology of the disease is not much different (all show varying degrees of what is known as mesodermal-glial reaction and neuronal necrosis and degeneration); clinical classification is not practical; most are arthropod-borne and therefore prevail in the warm seasons. Is it possible, then, that they had a common ancestor which was scattered over the world? Then, it might be postulated the environmental factors acted to impress certain changes on the viruses as revealed now by specific serological and immunity reactions. Such a factor may be in part the particular insect vector or reservoir animal in the invaded area to which the virus became adapted. The problem may be linked with a somewhat analogous one present in the global epidemiology of the rickettsioses (the ''typhus'' group of diseases). Here we have European (classical) typhus, louse-borne; New World typhus, flea-borne; Kenya (East African) typhus, tick-borne, and Far East typhus, mite-borne—all typhus, yet each one somehow distinct.

THE CHROMOSOMES OF POLYGYRID SNAILS[1]

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INTRODUCTION

PULMONATE gastropods are of considerable interest to students of variation and distribution, but in recent years only twenty-nine species have been examined critically enough by cytologists to warrant a statement as to the number of their chromosomes (White, 1940). This meager amount of information in a group so large has in part led us to undertake a preliminary study of the chromosomes of land snails in connection with the preparation of a check list of Virginia mollusks by one of us (P. R. B.). Similar studies of other groups of hermaphroditic animals—the Rhabdocoelida (Ruebush, 1938), the Cestoda (Jones, 1943) and the Trematoda (Britt, 1944)—have recently been made.

The chromosome numbers which can be regarded as reliable in species of the Pulmonata range from 17 haploid to 31. The highest is not high enough to be a multiple of the lowest and in between the two extremes the following numbers occur: 18, 20, 21, 22, 23, 24, 25, 26, 27, 29 and 30 (White, 1940). This nearly unbroken series suggests that the chromosome number has been altered *gradually* by the duplication or elimination of existing chromosomes, with or without change in structure, rather than by any *sudden* increase as would result from the duplication of the entire complement (polyploidy).

A survey of the literature and our own observations show that, even within species, there is a high degree of

aneuploidy.[2] This demands a detailed analysis of individuals, as was carried out by Naville (1923) and the Perrots (1937) in *Helix pomatia*. We have completed such an analysis in two species (*Triodopsis tridentata* and *T. fraudulenta*) during a rather extensive study of the Polygyridae in southwestern Virginia.

This family is the most widely spread group of helicid snails in North America. It is represented in southern Alaska, British Columbia, eastern Canada, Mexico and in nearly all the United States. Although the species tolerate a wide range of ecological conditions, they are most frequently found in humid country. The majority are woodland snails. During the day they are found under stones, dead wood or leaves. At night or during periods of rain they forsake cover and wander about more freely (Pilsbry, 1940).

Four of the genera of the family are known in Virginia: *Stenotrema, Mesodon, Triodopsis* and *Allogona*. We were successful in collecting material of the first three of these. They are "eastern genera" with ranges that are nearly coincident. *Stenotrema* and *Mesodon* (subfamily Polygyrinae) are separated from each other on the basis of shell characters, and from *Triodopsis* (subfamily Triodopsinae) by differences in the reproductive organs (Pilsbry, 1940).

We have examined one hundred and twenty-seven snails representing eighteen species and subspecies of these three genera. One hundred and six of them have 58 chromosomes (diploid). The remainder, all one species of *Triodopsis,* have 58, 59, 60, 61(?), or 62. These

[2] In the family Endodontidae the haploid chromosome number ranges from 29–31. Some individuals of *Mesomphix oxycoccus* have 29 chromosomes and others 30; *Mesomphix cupreus, Discus patula,* and *Anguispira alternata* all have 31. In the family Succineidae, *Succinea ovalis* from Mount Desert Island and Princeton, New Jersey, has 20 chromosomes (Hickman, 1931). The five individuals of this species we have seen from southwestern Virginia have 21. In the Polygyridae, *Polygyra appressa* (= *Mesodon appressus*, Pilsbry, 1940) from Burlington, New Jersey, has 31 chromosomes according to Pennypacker (1930), while the snails of this species we have examined from Virginia have only 29.

have been studied with respect to frequency of occurrence and distribution. Considerable attention has been paid to a heteromorphic bivalent found in four closely related species and subspecies.

Methods of Preparation

Snails were collected during July, August and September. The shell of each was wiped dry and the top whorl removed with a sharp bone scalpel. Pieces of the ovotestis, exposed as a white swollen mass in the upper whorl of the shell, were removed and submerged immediately in fixative. The procedure from the time the scalpel entered the shell until the material was in the fixative was completed in less than thirty seconds. After removal of the ovotestis the snails were preserved individually in 70 per cent. alcohol.

The ovotestis was fixed in medium Flemming and the fluid of Sanfelice (1918) for sectioning, and Carnoy for smearing (Painter, 1939). Material fixed for sectioning was either stained by means of the Feulgen reaction in bulk prior to complete dehydration or embedded for subsequent staining in crystal violet.

The following routine method gave excellent results without the time-consuming search for divisions the smear method entailed: Pieces of ovotestis were fixed in Sanfelice for from four to five hours, washed in five changes of 70 per cent. ethyl alcohol, and stained in Leuco-basic-fuchsin after from fifteen to thirty minutes hydrolysis in normal HCl at 58° C. Following staining and bleaching, the tissue was dehydrated in ethyl alcohol, cleared in chloroform and embedded in paraffin. Material of all species of the Polygyridae was satisfactory when sectioned at a thickness of 15 μ.

Observations were made with a Zeiss microscope equipped with 7–30 × oculars and a 90 × (n.a. 1.4) oil immersion objective. The chromosomes were drawn with the aid of a camera lucida and are reproduced at a magnification of 3290 ×.

TABLE 1

Collection number	Species	Chromosome number N	Chromosome number 2N	Number with heteromorphic bivalent	Number of individuals examined	Source
96	Stenotrema spinosum	29	58	0	2	Scott Co., Speer's Ferry
32*	S. stenotrema	29	58	0	2	Giles Co., Doe Mountain
30	S. hirsutum	29	58	0	2	Giles Co., Doe Mountain
58a	S. monodon aliciae	29	58	0	1 } 3	Giles Co., Salt Pond Mountain
58b	S. monodon aliciae	29	58	0	2	Giles Co., Clover Hollow
38*	Mesodon thyroidus	29	58	0	2	Pulaski Co., Radford
73	M. mitchellianus	29	58	0	2	Montgomery Co., Radford
20*	M. andrewsae normalis	29	58	0	1	Giles Co., M. L. B. Station
46*	M. zaletus	29	58	0	2	Pulaski Co., Radford
37*	M. appressus	29	58	0	2	Patrick Co., Meadows of Dan
64	M. rugeli	29	58	0	2	Giles Co., Newport
43	M. inflectus	29	58	0	1	Pulaski Co., Towes Ferry
34*	Triodopsis dentifera	29	58	0	2	Giles Co., Doe Mountain
21*	T. albolabris	29	58	0	3	Giles Co., Doe Mountain
22*, 60	T. fraudulenta	29, 29½, 30, 31	58, 59, 60, 62	4, 2, 3, 1	6, 6, 9, 1 } 23	Giles Co., Doe Mountain
67, 85, 90	T. fraudulenta	29, 29½, 30	61 or 62, 59, 60	6, 6, 6	26 } 30	Giles Co., Clover Hollow
40*	T. f. vulgata	29	60	0	2	Pulaski Co., Radford
62	T. f. vulgata	29	58	0	2 } 9	Giles Co., Newport
66	T. f. vulgata	29	58	0	4, 3	Giles Co., Hoge's Sink Hole
39	T. tridentata	29	58	2	3	Patrick Co., Meadows of Dan
23*, 55u–z	T. t. juxtidens	29	58	1	9 } 29	Giles Co., Doe Mountain
55a–m	T. t. juxtidens	29	58	5	4, 7	Giles Co., Doe Mountain
55n–t	T. t. juxtidens	29	58	0	7	Giles Co., Hoge's Sink Hole
24*, 61	T. t. edentilabris	29	58	3	12 } 16	Giles Co., Doe Mountain
61a	T. t. edentilabris	29	58	0	4	Developed in laboratory from juveniles, source unknown

* Identified by J. P. E. Morrison, U. S. National Museum.

Authorities for the taxonomic names found in Table 1 and throughout the text are found in the monograph of Pilsbry (1940).

OBSERVATIONS

Eighteen species and subspecies of the Polygyridae, with the exception of certain individuals to be described later, were found to have 29 pairs of chromosomes (Table 1). The chromosomes of *Stenotrema spinosum* (Fig. 1), *S. hirsutum* (Fig. 2), *S. monodon aliciae* (Fig. 3) and *S. stenotrema* (Fig. 4) are so similar that complements
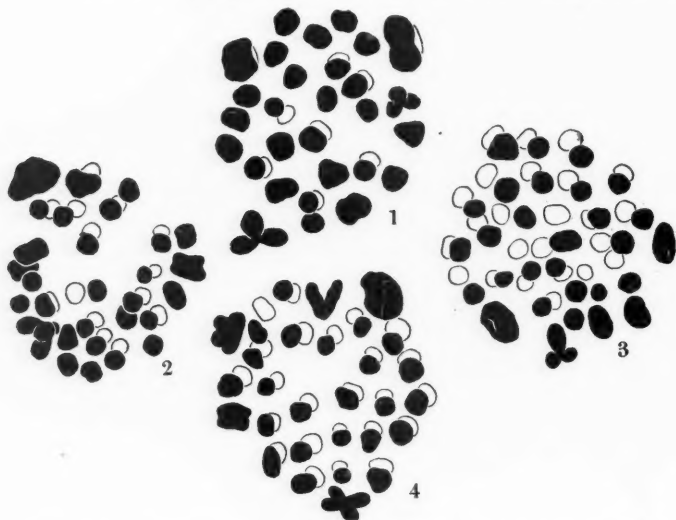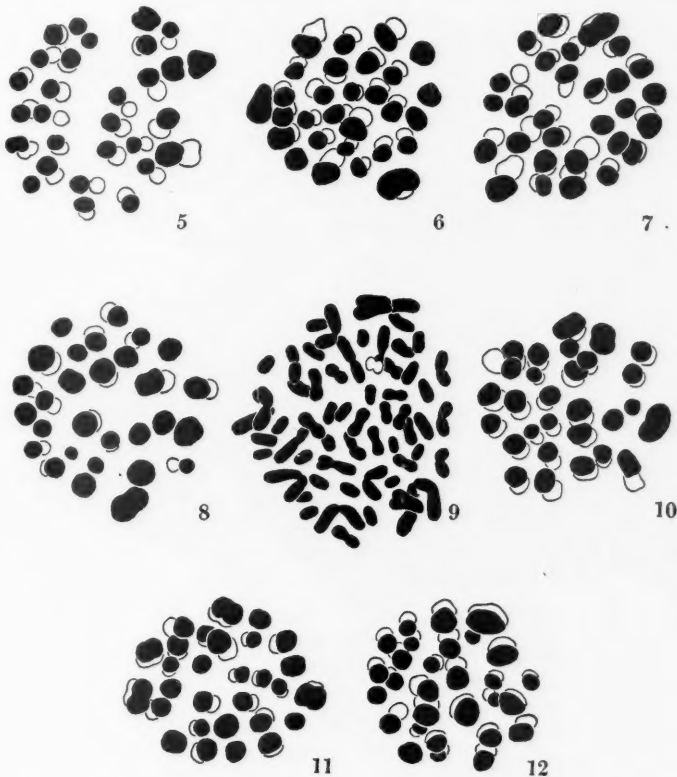

FIGS. 1–4. The chromosomes at metaphase-anaphase I of four species of Stenotrema. FIG. 1. *Stenotrema spinosum.* FIG. 2. *S. hirsutum.* FIG. 3. *S. monodon aliciae.* FIG. 4. *S. stenotrema.*

of the four can not be said to differ. In each species one bivalent is considerably larger than the others. The nine individuals representing these species all have chromosomes which are usually slightly larger than those of *Mesodon* and *Triodopsis* and less crowded on the spindle at metaphase I. The most striking difference between the chromosomes of species of *Stenotrema* and the other species of the family is the frequent occurrence of one or

more bivalents with interstitial chiasmata at metaphase. In the closely related *Mesodon* and in *Triodopsis* chiasmata are completely terminal or nearly so at diakinesis and later stages.

Twelve snails representing seven species of *Mesodon*

FIGS. 5–12. The chromosomes of seven species of Mesodon. FIG. 9 shows a spermatogonial metaphase, the others meiotic chromosomes at metaphase or early anaphase I. FIG. 5. *Mesodon thyroidus.* FIG. 6. *M. mitchelleanus.* FIG. 7. *M. andrewsae normalis.* FIGS. 8 and 9. *M. zaletus.* FIG. 10. *M. appressus.* FIG. 11. *M. rugeli.* FIG. 12. *M. inflectus.*

(Table 1 and Figs. 5–12) and 85 of the 106 representing seven species and subspecies of *Triodopsis* (Figs. 13–19 and 21) have the same number of chromosomes as *Steno-*

trema. The chromosomes in these two genera are so alike that a description of one applies equally well to the other. In all the species one pair of chromosomes is
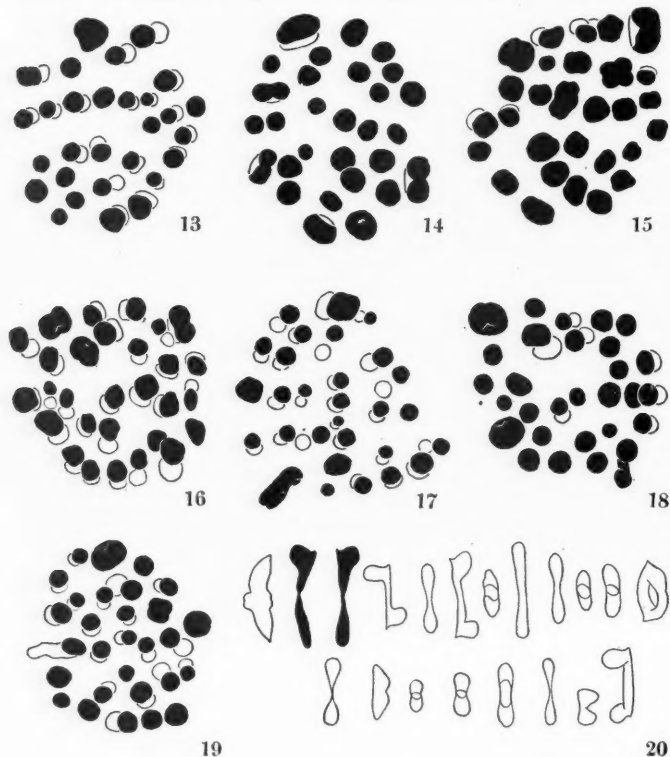

FIGS. 13–20. The chromosomes of seven species and subspecies of Triodopsis. FIGS. 17, 18 and 19 show a heteromorphic bivalent in polar view. FIG. 13. *Triodopsis fraudulenta vulgata.* FIG. 14. *T. albolabris.* FIG. 15. *T. dentifera.* FIGS. 16 and 17. *T. tridentata.* FIG. 18. *T. t. juxtidens.* FIG. 19. *T. t. edentilabris.* FIG. 20. Some of the bivalents in side view from a cell of *T. fraudulenta.* Two of these are heteromorphic.

larger than the others. Those comprising this pair ·in *M. zaletus* (Fig. 9) are approximately 4.8 μ in length at metaphase of the last spermatogonial mitosis and are at least six times the length of the smallest chromosomes.[3]

[3] In all members of the family the spermatogonial divisions are unsuitable for the determination of chromosome number. The spindle is of small diame-

The longest chromosomes, usually found at the periphery of the spindle, are easily detected. These show no tendency to be paired. The smallest chromosomes are likewise unpaired and are not confined to the central portion of the spindle to the exclusion of other size groups.

In the primary spermatocytes the large bivalents tend to be located at the edge of the spindle. Occasionally a large bivalent occupies the interior portion of the group where it reveals a strong body repulsion, forcing the other chromosomes toward the periphery (Fig. 23). A bivalent sometimes fails to be included on the spindle. Frequently one may be found on the spindle but unoriented. The
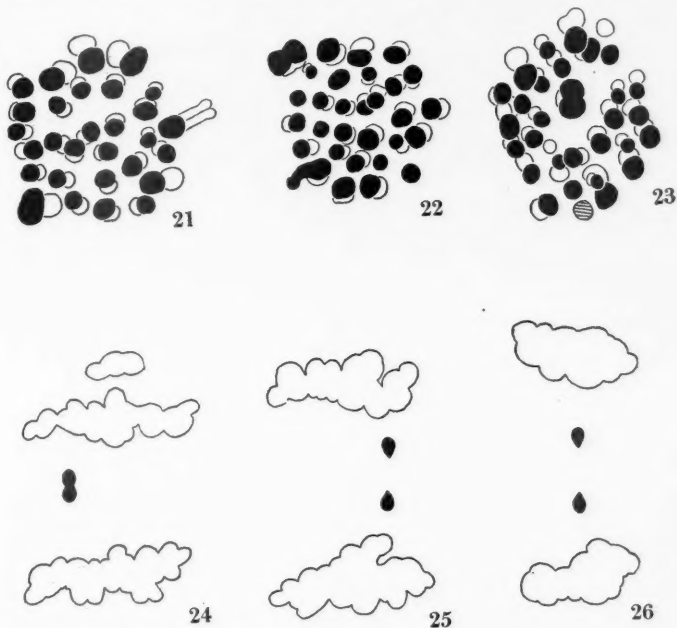
FIGS. 21–26. The chromosomes of *Triodopsis fraudulenta* at metaphase and anaphase I. FIG. 21. Twenty-nine bivalents (one heteromorphic). FIG. 22. Thirty bivalents (one heteromorphic). FIG. 23. Twenty-nine bivalents and one univalent. FIGS. 24–26. Division of a univalent during anaphase I.

ter; the chromosomes are crowded at metaphase and are frequently overlapping. The second meiotic division is also unsuitable but to a less extent.

chromosomes are regularly associated by one or two
chiasmata which are terminal at metaphase, or nearly so,
with the result that an interstitial chiasma is rarely seen
in polar view. There is a tendency, however, for the
smaller chromosomes to separate at anaphase before the
larger, and frequently separation begins before the chro-
mosomes have been brought to lie in one plane.

In none of the species of *Mesodon* and *Triodopsis,* with
the exception of *T. fraudulenta* (Fig. 31), has a partial
failure of meiotic pairing been observed which would lead
to univalent formation. Occasionally complete failure
occurs which results in the equational division of the
nucleus of the primary spermatocyte. Bivalent interlock-
ing has been seen in *Triodopsis albolabris* and *Triodopsis
tridentata juxtidens.*

Although multivalents have not been seen, a single
observation suggests that the absence of associations in-
volving more than two chromosomes does not necessarily
indicate an absence of homology between more than two
chromosomes of the complement. In one cell of *T. fraudu-
lenta* two heteromorphic bivalents were found (Fig. 20)
which are unlike those to be mentioned below. These two
are identical in that both are made up of a rod-shaped
chromosome associated by a terminal chiasma with a
larger approximately medianly constricted V-shaped
chromosome. The rod-shaped chromosomes appear iden-
tical, as do those which are medianly constricted. It
appears likely that there is some degree of chromosome
duplication here, as is implied in the suggestion above
that the seriation in chromosome numbers in the Pul-
monata is the result of an addition of chromosomes one
or a few at a time.

Of the 106 representatives of *Triodopsis* examined, the
remaining 21, all specimens of *T. fraudulenta,* have more
than 29 pairs of chromosomes (Table 1). Fifty-three
snails of this species have been studied; 23 from Doe
Mountain and 30 from nearby Clover Hollow. In Clover
Hollow four of the 30 snails (approximately 13 per cent.)

have either one or two extra chromosomes. In the two localities taken together nearly 40 per cent. of the snails have a chromosome number greater than that found in the other species of the family. Sixty per cent. have the characteristic number, 58; 21 per cent., 60; 15 per cent., 59; and two snails or ca. 4 per cent. have 61(?) or 62[4] chromosomes. Fig. 21 shows the metaphase-anaphase I chromosomes of a snail with 29 bivalents. Fig. 22 shows the chromosomes of another snail with 30 bivalents, and Fig. 23 the chromosomes of a third snail with 29 bivalents and 1 univalent or 59 chromosomes. The snails with 60 chromosomes regularly show 30 bivalents and no multivalent associations. Those with 59 chromosomes show 29 bivalents and 1 univalent. The univalent is usually found at the periphery of the spindle or between the equatorial region and one pole. It is either moved to one pole as the bivalents separate at anaphase or begins to divide during anaphase (Fig. 24). Separation of the halves is accomplished prior to late anaphase (Fig. 25) and movement of these toward the poles is well under way before telophase (Fig. 26). Because of its behavior and greater translucence *in polar view* the univalent is easily found. An acquaintance with it eliminates the possibility that the snails interpretated as having 30 bivalents or more represent individuals in which failure of meiotic pairing occurs.

When snails with extra chromosomes were first found no record had been kept as to the exact origin of each individual. During 1943 collections were made within three small but well-separated areas on Doe Mountain to determine whether the variation in number was widespread or localized. Stations were designated 1–3 from lowest to highest altitude (4,200 feet). At Station 1, near the intersection of Giles County Highways 613 and 614, one snail with 58, three with 59 and four with 60 chromosomes were found. Along Hemlock Branch near Highway 614 (Station 2), two individuals with 58, two with 59,

[4] One of these is a mosaic with cells containing 62, 64 and 66 chromosomes. The other has too few divisions for a complete analysis. It has either 61 or 62 chromosomes.

and one with predominantly 62 chromosomes were col-
lected. At Station 3 on the southwestern slope from the
flat summit, one snail with 59 chromosomes and three with
60 occurred. It is clear that the number variants are
distributed widely and intermingle at least along the
western slope of this mountain.

One snail from Station 2 is of considerable interest in
that it shows a variation in chromosome number within
the individual. The ovotestis, only a portion of which
was fixed, contains 12 primary spermatocytes suitably
oriented for a study of metaphase or anaphase in polar
view. Eight of these have 31 pairs of chromosomes. The
chromosomes of one with 31 bivalents are shown at early
anaphase in Fig. 27 and those of another at late anaphase
with 31 chromosomes toward opposite poles in Fig. 30.
Two cells have 32 bivalents (Fig. 28) and two others 66
chromosomes. One cell with 66 chromosomes is at early
anaphase. It has 32 bivalents and 2 univalents (Fig. 29);
another, at late anaphase, has 33 chromosomes toward
each pole (Fig. 32). In *T. fraudulenta* snails with 62
chromosomes occur if it is assumed that the eight cells
with this number represent the true composition of the
snail described above and that the higher numbers are
derived from this by an increase during or before the for-
mation of the ovotestis.

To determine if a small increase in the number of chro-
mosomes results in an increase in the size of the nucleus,
100 nuclei at diakinesis were drawn with the camera
lucida from each of three snails with 58, 60 and 62 or more
chromosomes respectively. The nuclei at diakinesis are
not always spherical so the average of the shortest and
longest axis was taken as the diameter. The differences
in diameter were not statistically significant. If an in-
crease in nuclear volume accompanies a small increase in
the number of chromosomes it is not of sufficient magni-
tude to be readily detected.

In certain representatives of two species examined, one
of the bivalents is made up of chromosomes which are of
unequal size. The two species in which this hetero-

morphic bivalent is found are *T. tridentata* and *T. fraudu-lenta*[5] (Table 1).   In the former 15 of the 39 individuals which were examined showed a heteromorphic bivalent. This was found in *T. t. tridentata*, *T. t. juxtidens*, as well as in *T. t. edentilabris*.   In the latter all nine representa-
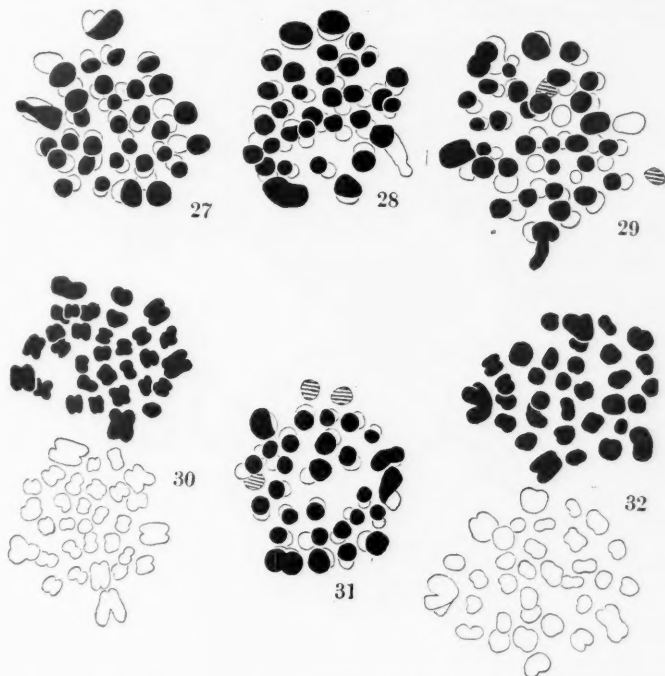
FIGS. 27–32.   The chromosomes of *Triodopsis fraudulenta* at metaphase and anaphase I.   With the exception of FIG. 31, all are from the same ovotestis.   FIG. 27.   Thirty-one bivalents.   FIG. 28.   Thirty-two bivalents. FIG. 29. Thirty-two bivalents and two univalents or sixty-six chromosomes. FIG. 30.   Thirty-one chromosomes toward each pole at anaphase I.   FIG. 31. Twenty-eight bivalents and three univalents.   FIG. 32.   Thirty-three chromosomes toward each pole at anaphase I.

tives of the typical widely distributed *T. f. vulgata* contained only chromosomes of equal size associated, but 16

[5] It happens that these two species are the ones sampled most extensively. To what extent the failure to find a heteromorphic bivalent elsewhere can be attributed to lesser sampling is not known.

of the 53 individuals of the specialized local race *T. fraudulenta* showed a heteromorphic bivalent.

This bivalent is of a constant occurrence within an individual. It can be detected easily in polar view of metaphase-anaphase I (Figs. 17–19, 21, 22, 27–29) and, when suitably oriented, in side view (Figs. 33, 34). It is almost invariably found at the edge of the spindle. A somewhat weaker staining reaction sometimes encountered in the free arm of the larger chromosomes, as well as what appears to be a loose coiling, suggests that the hetero-

33

34

FIGS. 33 and 34. Heteromorphic bivalents from individuals of *Triodopsis tridentata* and *T. fraudulenta*. FIG. 33. Heteromorphic bivalents from individuals of (a) *T. t. tridentata*, (b) *T. t. juxtidens*, and (c) *T. t. edentilabris*. FIG. 34. Heteromorphic bivalents from twelve specimens of *T. fraudulenta*.

morphism results from a differential contraction of an unpaired part. This interpretation is not established, however, since the less intense staining is not a constant feature, and chromosomes which appear contracted to the same extent and still unequal in size are found associated (Figs. 33a and b).

Fig. 16 shows, in polar view, the chromosomes from an individual of *T. t. tridentata* lacking the heteromorphic bivalent and Fig. 17 those from one of the two individuals which have this bivalent. Fig. 33a shows heteromorphic bivalents in side view selected from two of the individuals. These three snails, two with a heteromorphic bivalent and

one without, are from the Meadows of Dan, Patrick County, Virginia, which is approximately 40 miles from the region in Giles where *T. t. juxtidens* and *T. t. edentilabris* were found.

Eight of the 20 individuals of *T. t. juxtidens* have a heteromorphic bivalent (Figs. 18 and 33b), and five of the 16 individuals of *T. t. edentilabris* (Figs. 19 and 33c). The *T. t. juxtidens* with a heteromorphic bivalent was found in two regions of Giles County, on Doe Mountain and at Hoge's Sink Hole. The *T. t. edentilabris*, with a bivalent that is similar in size, shape and position on the spindle, was found along with *T. t. juxtidens* on Doe Mountain. Snails of both subspecies with a heteromorphic bivalent have been found during two seasons in this locality. With regard to shell characters they are indistinguishable from the other snails.

In *T. fraudulenta* the heteromorphic bivalent is similar to the one in *T. tridentata* but not always uniform in appearance (Figs. 21, 22, 27–29 and 34). On Doe Mountain 10 of the 23 snails of this species examined (approximately 47 per cent.) show this bivalent. The *T. tridentata* forms with an unequal pair of chromosomes occur with a frequency of about 40 per cent. on the same mountain. In Clover Hollow, which is at least five miles from Doe Mountain, only six of the 30 snails of *T. fraudulenta* examined had a heteromorphic bivalent. Individuals with a heteromorphic bivalent can not be distinguished by shell features from those with the chromosomes of each pair of equal size. In this species, the heteromorphic bivalent has been found in 1941, 1943 and 1944. The chromosomes are usually associated by a chiasma betwen the short arm of the longer chromosome and the smaller which results in a disjunctional separation of chromosomes of unequal size at anaphase I. Two cases have been seen, one of which is shown in Fig. 34, which may be interpreted as a chiasma involving the long arm of the longer chromosome which will result in an equational separation of the longer segment at anaphase I.

DISCUSSION

The number of species from the three genera of the Polygyridae we have seen warrants the conclusion that the chromosome number characteristic of the family in southwestern Virginia is 58.

Two species, *Triodopsis fraudulenta* and *T. tridentata*, have been sampled more extensively than the others. *T. fraudulenta* is a "specialized local race of . . . *T. f. vulgata.*" It occurs only "in the ranges along the Virginia and West Virginia boundary and a little farther east" (Pilsbry, 1940, p. 805). *Triodopsis tridentata* is a widespread eastern species ranging, according to Pilsbry (p. 796), from Ontario and New England south to Georgia, Alabama, Mississippi and west to Illinois, Indiana and Kentucky. *Triodopsis tridentata edentilabris* appears to be a "doubtful" form of *tridentata* differing only in the total absence of teeth in the lip. Pilsbry (1940, p. 797) writes: "Specimens with toothless, or almost toothless lip occur rarely among normal *tridentata*. F. C. Baker found specimens in which 'the peristome is perfectly plane and rounded' at Rochester, N. Y., which he described as *P. tridentata unidentata*. Dr. V. Sterki remarked that 'specimens from various places (in Ohio) have the peristome without teeth, or with mere traces of such, but do not constitute a variety.' Whether the specimens I described as *edentilabris* over forty-five years ago are such individual mutations, or a little local race, is still uncertain." *Triodopsis tridentata juxtidens,* according to Pilsbry (1940, p. 799), is a race "common in the hilly northern part of New Jersey and along the Delaware southward, in the eastern half of Pennsylvania, west to Somerset County, in the south . . . . It extends through Maryland, Virginia, North Carolina and as far south as Berkeley County, South Carolina."

"Most subspecies," Pilsbry (1939, XIV) writes, "are recognizably differentiated populations which are not considered sufficiently distinct to be called species. They are merely incipient species, in which the discontinuity is incomplete, or is not strongly pronounced. In some cases,

that of *Triodopsis tridentata juxtidens,* for example, the geographic or ecologic segregation which a subspecies should have is not evident. Such subspecies are much in need of further study.''

In *T. fraudulenta* and *T. tridentata* a heteromorphic bivalent occurs in certain individuals. The frequency of occurrence is of much the same order in the two species, though in *fraudulenta* there is evidence of a difference in frequency in localities separated by only a few miles. The specialized local race, *T. fraudulenta,* appears to be distinguished from the typically widely spread form of the species, *T. f. vulgata,* by a fairly high frequency of individuals carrying this bivalent. To that extent its recognition as a distinct taxonomic unit seems justified. On the other hand, in *T. tridentata* the subspecific categories, *edentilabris* and *juxtidens,* appear to be of doubtful validity. In these the frequency of individuals with a heteromorphic bivalent is relatively the same.

In *tridentata* and its subspecies the bivalents are uniform in appearance while in *fraudulenta* some variation is seen. In both species they are usually found at the periphery of the spindle at Metaphase I. In this respect their behavior is similar to the sex bivalent in many animals.[6]

Heteromorphic bivalents not associated with sex appear to be of less frequent occurrence than the numerous descriptions in some groups might suggest. In the Polygyridae they are found in two closely related species in southwestern Virginia. It is tempting to attribute this to the interbreeding of the forms involved. This is especially so since *T. t. edentilabris, T. t. juxtidens* and *T.*

[6] Sex chromosomes have been described in several pulmonate gastropods: *Helix pomatia* (Demoll, 1912), *Limax maxima, L. tenellus, L. cinereoniger, Agriolimax agestris* and *Lehmannia marginata* (Perrot, 1930). As pointed out by Whitney (1940), ''the manner in which these operate to determine sex remains . . . somewhat hypothetical.'' The X-chromosome of Perrot, as seen in his figures 61–69, can be interpreted as a bivalent which has failed to become oriented on the spindle. This situation is occasionally encountered in nearly all species of the Polygyridae. There is no evidence that the heteromorphic bivalents here described are in any way associated with sex determination in their hermaphroditic organisms.

fraudulenta are found together on Doe Mountain.   The *edentilabris* and *juxtidens* may be interbreeding forms, but it is unlikely that *fraudulenta* is a part of such a population, for *edentilabris* and *juxtidens* have only 58 chromosomes, while *fraudulenta* has 58, 59, 60, 61(?) or 62. This situation may be of further significance. *Triodopsis fraudulenta* is a local race of a comprehensive category. If by any chance this local race constitutes a population which, though not crossing now with related forms, is the result of interbreeding between two species, then deviation from a characteristic chromosome number might well occur.

Any speculation as to the part played by an increase in chromosome number due to polyploidy in the Pulmonata seems premature. *Helix pomatia* has long been considered a possible polyploid since the numbers 12 and 24 were reported from this species by several early workers (*cf.* review of literature by Perrot and Perrot, 1937). Later studies revealed 18 chromosomes in 33 animals from Geneva (Naville, 1923) and 27 in all the snails from two continents examined by Perrot and Perrot (1937). The results of Naville, which have not been confirmed, must be considered doubtful since in certain acini of five animals he found nuclei containing 27 bodies, the number regularly encountered by later workers in this and two related species. If the results of Naville can be confirmed it would be possible, as Perrot and Perrot have pointed out, to consider Naville's race a tetraploid and the other snails hexaploid. If this is the case a land snail with a chromosome number low enough to be a diploid has not as yet been found.

The haploid number of *Helix pomatia* is probably not 12, 18 or 24 but 27. Perrot and Perrot (1937, p. 206) state: "De très nombreuses numérations effectuées sur des prophases tardives ou diakinétiques, sur des méfaphases de première et de deuxième division de maturation et sur quelques anaphases ont toujours montré 27 éléments chromatiques dans la lignée mâle." Whether the number is invariably 27 is open to question in the light

of the present study. This is especially so since one metaphase II figured by Perrot and Perrot, contrary to the statement above, shows clearly 28 chromosomes.

In the Polygyridae in Virginia the chromosome number is 29. *Mesodon appressus* represented by two different snails has this number, but in New Jersey an unstated number have 31 (Pennypacker, 1930). The extra chromosomes found in several individuals of *T. fraudulenta* are not the smallest chromosomes. They are identical in staining reaction and behavior to the others of the complement. Snails containing them are well established in the region where they occur and, like the trisomic grasshopper of Callan (1941), are morphologically indistinguishable from those with the usual number of chromosomes. The extra chromosomes, however, do not resemble inert fragment-, or b-chromosomes but appear as duplications of other chromosomes of the complement. Whether they arise by non-disjunction or misdivision and isochromosome formation is impossible to determine in this material. It is clear that fragmentation such as Troedsson (1944) has postulated to explain the origin of supernumerary X-chromosomes does not play a part here where a localized centromere is found on each chromosome.

In the mosaic individual, cells occur with 62, 64 and 66 chromosomes. The cells with 62 and 64 have their chromosomes paired as bivalents. The cell with 66 chromosomes at early anaphase has these, as would seem more likely, associated as 32 bivalents and 2 univalents. It is difficult to understand how the addition of a *pair* of homologous chromosomes to form another bivalent is accomplished in premeiotic tissue where there seems to be no tendency toward somatic pairing, unless there is considerably more duplication in these animals than one is led to suspect from a search for multivalent associations.

The mosaic *fraudulenta* suggests that individuals of this species can be expected with as many as 66 chromosomes, or eight more than the number characteristic of

the family. The evidence for a gradual increase in chromosome number, presented here for a single species, suggests that in the Pulmonata as a whole the progressive increase from 34 to 62 chromosomes may be attributed entirely to the duplication of chromosomes one or two at a time rather than to a sudden doubling of the complement and subsequent loss. It appears that this organism can tolerate recurrent duplication of chromosome elements. The mechanism by which this gradual increase is accomplished is unknown, but in future investigations the possibility that a one-time hybridization between differentiating populations is concerned should not be ignored.

The addition of a pair of chromosomes in duplicate alters little the volume of the nucleus. With the intervention of a period of adjustment, a period during which selection may act to reduce volume, a state may be established in time which approaches and is comparable to polyploidy. This, somewhat contrary to a frequently stated conclusion, may eventually result in greater variability for the amount of mutatable material has been increased.

Summary

Eighteen species and subspecies in three genera of the Polygyridae were found to have 58 as the typical chromosome number. The chromosomes of *Mesodon* (Polygyrinae) resemble more closely those of *Triodopsis* (Triodopsinae) than those of *Stenotrema* (Polygyrinae).

Two species were extensively sampled. In *Triodopsis fraudulenta* a frequently encountered variation in chromosome number occurs. Individuals have 58, 59, 60, 61(?) or 62 (diploid) chromosomes. It is suggested that snails can tolerate recurrent duplication of chromosome elements, and that in the Pulmonata as a whole, the nearly unbroken seriation in chromosome number may be attributed to a gradual increase from 34 to 62. In *T. fraudulenta* snails with extra chromosomes show no detectable increase in the volume of their nuclei nor can they be distinguished morphologically from those with the number of chromosomes at present characteristic of the family in Virginia.

In two species (*T. fraudulenta* and *T. tridentata*) a single heteromorphic bivalent occurs in approximately 40–47 per cent. of the individuals examined. The frequency of occurrence of this bivalent, and also extra chromosomes appear to be a locality characteristic within *fraudulenta*. In this species the occurrence or non-occurrence of the heteromorphic bivalent is correlated with a taxonomic distinction which may also be justified on morphological and ecological grounds. In *T. tridentata* there is no striking difference in frequency of the heteromorphic bivalent between subspecific categories which on other grounds appear to be of questionable validity.

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YIELD GENES, HETEROSIS AND COMBINING ABILITY[1]

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A WIDE collection of varieties of almost any crop plant often exhibits a wide range in variability for each quantitative character. Yield and other quantitative characters usually are the end result of the interaction of a large number of genes under particular environmental conditions. What is inherited is the manner of reaction and not the character itself.

A recent review of quantitative inheritance studies has been made by Smith (1944). All that will be attempted in relation to yield inheritance will be a condensed summary of various types of gene action and interaction that may be considered under the heading of yield genes.

Yield Genes. Resistances to plant diseases are of great importance in relation to yield. The various types of inheritance of disease reaction may be used as one illustration of the genetic complexity of this factor in yield. For a disease such as stem rust of wheat caused by *Puccinia graminis tritici* there are many physiological races of the pathogen that are differentiated by their reaction on a series of host varieties and species of wheat. Some varieties of wheat are resistant under field conditions from heading to maturity in the spring wheat area of North America to all or nearly all races of stem rust, which has been called mature plant resistance. This resistance in certain crosses where Hope or H-44, or their derivatives, are used as one parent is dominant in F_1 over susceptibility and the reaction in the segregating generations is dependent upon one or two factor pairs. · This

type of resistance was obtained from *Triticum dicoccum*. Where the Thatcher type of mature plant resistance, obtained originally from *T. durum*, is studied in crosses with a susceptible variety, susceptibility is dominant in F_1 and resistance in F_2 may be explained by the complementary action of two genetic factors in the homozygous recessive condition. When dealing with true protoplasmic resistance to stem rust of wheat, which functions throughout the life of the plant, to only a single race of the organism, the manner of inheritance of reaction to rust may be explained by one or more factor pair differences. In some cases a single factor pair may condition reaction to several races of stem rust. Since there are approximately 200 physiological races of the pathogen, the number and nature of this group of yield genes gives some idea of the complexity of yield inheritance.

Chlorophyll is essential to the manufacture of food by the plant. There are over 100 genes that have been isolated in corn that affect chlorophyll development. The recessive condition of any one of these genes leads to abnormal development. Is it logical to conclude that the interaction of these 100 dominant genes, each located at a different locus in the chromosome map, is essential to normal chlorophyll development in corn?

There are several different dwarfs in corn that are each dependent upon the recessive condition of a single factor pair. A cross between two different dwarfs gives normal growth in F_1. Each of these recessive dwarfs suppresses the expression of other growth factors to a marked degree.

Genetic diversity of origin of factors conditioning yield is as important in self as in cross pollinated plants. The introduction of Bond and Victoria oats brought in factors for disease resistance and in addition other genes that were different from those already available for standing ability, kernel quality, etc., that appear in some crosses to be complementary to genes already available. New varieties of oats with Bond or Victoria as a parent are responsible for large increases in the yielding ability of oats.

These illustrations may serve to emphasize the fact that the number and nature of genes influencing yield is very great. In some cases genes for quantitative characters appear to be additive, while in "other cases the gene substitution multiplies the residual genotypic value by a certain amount" and is said to have geometric action. Other cases of intermediate action are known. Genes of a complementary nature where each alone has no apparent effect may be classified as yield genes. Cases where a homozygous recessive partially or wholly suppresses the interaction of other genes also are of importance in yield inheritance.

A brief discussion of heterosis from the genetic standpoint may serve to furnish a basis for the discussion of combining ability.

Heterosis. In cross-pollinated plants certain yield genes and growth factors are in a heterozygous condition while other important yield genes are homozygous. Differences in the growth habit and yield of inbred lines of corn result from the interaction of different genes in the homozygous condition. When two different inbred lines of corn are crossed often great hybrid vigor results. Heterosis is a term first used by Shull (1914) in 1914 instead of the phrases "stimulus of heterozygosis," "the stimulating effect of hybridity," etc., to avoid, as he said, "the implication that all the genotypic differences that stimulate physiological activities of an organism are Mendelian in their inheritance and to gain brevity of expression." The excellent review by Whaley (1944) of "Heterosis" is well known. The most satisfactory genetic viewpoint is that "heterosis" and hybrid vigor are phases of quantitative inheritance and explained on the basis of dominance as suggested by Keeble and Pellew (1910), Bruce (1910) and clarified by Jones (1917) in the light of the great increase in knowledge of quantitative inheritance obtained during the period from 1910 to 1914. In addition to the dominance or partial dominance of growth factors as causing heterosis it seems evident, in

some cases, that complementary factors where the inter-
action of two or more factors is necessary to produce the
character, and the hypothesis of multiple alleles where the
heterozygous condition is more vigorous than the homo-
zygous, play a part also in causing hybrid vigor.   Illus-
trations of various types of manifestations of the heter-
ozygous condition may be of interest.

Powers (1944) presented in 1944 what he called an
expansion of Jones's theory for the explanation of heter-
osis.   He considers that heterosis and dominance are
different degrees of expression of the same "physiologi-
cal genetic phenomena."   If the term "heterosis" is to
be used in reference to definite characters of an organism
where the character of the hybrid is superior to the better
parent, or inferior to the weaker, then it seems that the
definition of heterosis must be on the basis of "manifes-
tation of heterozygosity" rather than "the stimulus of
heterozygosity."   It is apparent that dominance and
partial dominance also are manifestations of heterozy-
gosity.

The following diagram illustrates various manifesta-
tions of the heterozygous condition.

VALUES OF F_1 HYBRIDS AND PARENTS IN RELATION TO HETEROSIS AND
DOMINANCE (AFTER POWERS)

F_1 hybrid

```
          6 } —Heterosis
Parent 5   —Complete dominance
          4 } —Partial dominance
          3  —No dominance
          2 } —Partial dominance
Parent 1   —Complete dominance
          0 } —Heterosis
```

For any given quantitative character difference it is
evident that the hybrid may be superior to the stronger
parent or inferior to the weaker parent referred to in this
diagram as heterosis, equal to the parents called domi-
nance, or approaching one or the other parent called
partial dominance.

An illustration of three F_1 tomato crosses and their

parents gives some idea of the various types of expression of characters in the heterozygous condition.

In the first cross, according to Powers's terminology, number of ripe fruit and total yield show heterosis, and weight of ripe fruit partial dominance of heavy fruit over light. In the second cross there is one case of dominance, one of partial dominance, and one of heterosis. In the third cross there is partial dominance of a small number of ripe fruit and of small fruit size. In spite of this fact this cross shows heterosis for total yield of ripe fruit. Many illustrations are available in the literature of F_1

TABLE 1

NUMBER OF RIPE FRUIT, WEIGHT OF FRUIT AND YIELD OF RIPE FRUIT IN THREE TOMATO CROSSES (AFTER POWERS)

Hybrid or inbred	Ripe fruit (number)	Wt. in grams (ind. fruit)	Yield ripe fruit (gms)
4109	118	12	1364
F_1	183H*	16P.D.	2876H
4110	109	17	1868
4101	4	119	513
F_1	21D	89P.D.	1827H
4103	20	55	1066
4102	4	138	607
F_1	45P.D.S.	55P.D.S.	2428H
4110	109	17	1868

* H = heterosis, P.D. = partially dominant, D = dominant, P.D.S. = partially dominant smaller parent.

hybrids that are less vigorous than the smaller parent. Such a cross was pictured by East and Hayes (1912) between *Nicotiana tabacum* $\times$ *N. alta* where the hybrid was normal in appearance but only about one-tenth of the size of the smaller parent.

An illustration of heterosis (see Table 2) resulting from multiple alleles is taken from Oliver and Green (1944) where genes for lozenge eye in Drosophila have an effect on viability, fertility and fecundity of the females.

It is apparent that the heterozygous condition for various alleles of lozenge leads to greater variability, fertility and fecundity of the females than the homozygous. The control, or normal eye factor, however, is more vigorous than any combination of lozenge alleles.

Collins (1921) emphasized the importance of deleterious recessives in relation to heterosis. It is a well-known fact that F_1 crosses between a line with such a degenerate change and another line carrying an allele for normal growth often show complete dominance of the normal condition over the degenerate mutation. Such degenerate changes were classed as "physiologic defectives" by East (1936), who stated that these were the types of characters frequently used by students of genetics. Jones (1945) has given several illustrations of mutations of this nature that have occurred in long-time inbred lines of corn at the Connecticut station, each believed to have re-

TABLE 2

VIABILITY, FERTILITY AND FECUNDITY OF THE OFFSPRING OF FEMALES WITH DIFFERENT LOZENGE ALLELES

| ♀ type | Drosophila mel. | | (Oliver and Green) Fecundity Av. No. progeny |
	Viability per cent. alive	Fertility per cent.	
lz^g	83 ± 1	23 ± 2	9 ± 1
lz^s	29 ± 2	35 ± 4	15 ± 2
lz	40 ± 2	29 ± 3	8 ± 1
lz^g/lz^s	92 ± 1	49 ± 2	26 ± 1
lz^g/lz	82 ± 2	35 ± 2	21 ± 2
lz^s/lz	84 ± 3	48 ± 4	25 ± 2
control	90 ± 3	86 ± 3	61 ± 2

sulted from a single gene change. The title of Jones's most recent paper is "Heterosis Resulting from Degenerative Changes." Data of parents and crosses will be given to illustrate the nature of the results. It will be noted, as Jones states, that these mutations "reduce the vigor of the inbred plants but increase the growth of their hybrid offspring when they are crossed back to the normal line from which they were derived and from which they differ by what appears to be a single allele."

The illustration selected from Jones's studies consisted of a narrow-leafed mutation that occurred in an inbred line of C.I. 4–8. Data from the normal line C, the narrow leaf mutation and the F_1 cross are given in Table 3.

The mutation showed large heterosis in weight of ears when crossed with the normal inbred line from which it was obtained. Perhaps this is another illustration of

the action of multiple alleles with different physiological effects on the organism.

Degenerate lines and the normal lines from which they were obtained were crossed with normal unrelated lines with which the normal lines had given large increases in yield.   The data indicate that the mutated lines yielded as well in crosses, on the average, as the lines from which they originated.   Jones states that the results emphasize "the importance of caution in applying any rigorous selective elimination of degenerate individuals either in plant and animal breeding practice or in eugenic procedure."

It seems probable to the writer that most plant breeders will continue to practice selection for desirable charac-

TABLE 3

NORMAL C INBRED, NARROW LEAF MUTATION AND THE F₁ CROSS

Designation	Wt. of ears	Ht. of stalk	Leaf width	Date silked
Normal C	292	65.0	88.9	20
Narrow leaf	432	75.5	65.8	12
F₁ normal × narrow	873	79.4	82.5	14

ters and not worry over discarding desirable germ plasm that is suppressed by homozygous undesirable recessives. Such recessives, however, may be a possible source of desirable growth factors.   Richey, many years ago at a corn conference, suggested the possibility of using undesirable recessives as a source of desirable germ plasm, on the basis that if they survived they must carry other desirable factors to offset the undesirability of the so-called homozygous suppressor.

Combining Ability.   Combining ability is a term to denote the performance of clonal or inbred lines in comparable crosses.   A common method in corn is to use inbred-variety crosses to test combining ability of inbred lines of corn.   An equally satisfactory method appears to be to cross each inbred with several other inbreds used as testers and test these crosses for performance.   Several have suggested the use of special testers that are relatively undesirable in the character to be tested.

TABLE 4

NUMBER OF RIPE FRUIT PER PLANT OF INBREDS AND F₁ CROSSES IN TOMATOES (AFTER POWERS)

Variety or inbred	Number of ripe fruits (per plant)	
	Variety or inbred	9 crosses (av.)
4101	4.3 ± 0.3	20.8 ± 1.0
4102	4.4 ± 0.7	19.2 ± 0.6
4105	2.9 ± 0.6	19.4 ± 0.6
4106	8.8 ± 1.0	24.7 ± 1.0
4103	19.5 ± 2.9	35.4 ± 1.4
4104	15.5 ± 2.5	32.4 ± 1.2
4107	9.4 ± 1.5	23.6 ± 0.8
4108	10.7 ± 1.2	24.4 ± 0.9
4109	118.3 ± 12.9	81.9 ± 2.2
4110	109.1 ± 11.3	76.7 ± 2.2

Some have concluded that there is no very close relation between the characters of inbred lines and the yielding ability of their crosses. It may be well to study a few cases in both self- and cross-pollinated plants.

In tomatoes Powers (1945) studied the relationship of the characters of 9 inbred lines and of all possible F₁ crosses between these lines. Number of ripe fruit per plant, average weight of individual fruit and yield of ripe fruit per plant of the inbreds were compared with that of the crosses (see Tables 4 to 6).

Four of the inbreds in the upper part of each table were selected from varietal crosses within *Lycopersicum esculentum*. The other six inbreds were selected from species crosses of *L. esculentum × L. pimpinnelifolium*.

There is a rather strong relation between the number of ripe fruit of each inbred and of the average of its 9

TABLE 5

AVERAGE WEIGHT IN GRAMS OF INDIVIDUAL FRUIT OF INBRED LINES OF TOMATOES AND THEIR F₁ CROSSES (AFTER POWERS)

Variety or inbred	Mean weight grams (ind. fruit)	
	Variety or inbred	9 crosses (av.)
4101	119 ± 7	87 ± 2
4102	138 ± 13	84 ± 2
4105	114 ± 8	83 ± 2
4106	94 ± 6	75 ± 2
4103	55 ± 3	61 ± 1
4104	52 ± 3	60 ± 1
4107	85 ± 4	73 ± 1
4108	80 ± 3	74 ± 1
4109	12 ± 1	26 ± 0.4
4110	17 ± 1	34 ± 0.6

crosses. Average weight of fruit per plant in grams and total yield per plant also indicate a strong correlation between the average yield of each of the ten inbred lines and the average yield of their crosses obtained for each inbred by crossing it with the other nine inbreds.

Although, on the average, there is rather good agreement between the performance of inbred tomatoes and combining ability in crosses, it is apparent that the only sure way of testing the combining ability of inbred tomatoes is by comparable trials.

Numerous studies have been made of the relation be-

TABLE 6

YIELD OF RIPE FRUIT IN GRAMS IN TOMATOES (AFTER POWERS)

Variety or inbred	Yield of ripe fruits (per plant)	
	Variety or inbred grams	9 crosses (av.) grams
L. esculentum		
Bounty 4101	513 ± 39	1280 ± 53
4102	607 ± 86	1267 ± 46
4105	332 ± 64	1081 ± 33
4106	828 ± 108	1236 ± 45
Es. × *L. pim.*		
4103	1066 ± 159	1597 ± 54
4104	808 ± 114	1340 ± 44
4107	801 ± 111	1181 ± 47
4108	857 ± 108	1192 ± 41
4109	1364 ± 151	1968 ± 46
4110	1868 ± 149	2231 ± 52

tween the yielding ability of inbred lines of corn and of their combining ability in F_1 crosses. Only a few cases can be mentioned.

One hundred and ten inbred lines of corn selected from various sources, including selection from open-pollinated varieties and from definite crosses between inbreds, were studied at Minnesota (Hayes and Johnson, 1939) in relation to their performance in top crosses. The characters in replicated plots of the inbreds that were studied are as follows:

All possible correlation values were calculated between the characters of the 110 inbreds and each was correlated with inbred-variety yield (see Table 8).

All relations were significant at the 5 per cent. point except two correlations between pollen yield and charac-

TABLE 7

CHARACTERS OF 110 INBRED LINES OF CORN CORRELATED WITH
INBRED-VARIETY YIELDING ABILITY

1. Date silked	7. Stalk diameter
2. Plant height	8. Total brace roots
3. Ear height	9. Tassel index
4. Leaf area	10. Pollen yield
5. Pulling resistance	11. Grain yield
6. Root volume	12. Ear length

ters of inbreds and nearly all correlations between length of ear and other inbred characters studied. Length of ear, however, showed a significant association with inbred-variety yield. The characters most strongly correlated with inbred-variety yield included 1, date of silking; 5, pulling resistance; 6, root-volume; 7, stalk diameter; and 8, total brace roots.

The multiple-correlation value of all twelve characters of the 110 inbreds and inbred-variety yield was 0.67, indicating that under the conditions of the experiment 40 per cent. of the variability of inbred-variety yield was directly related to characters of vigor in the inbreds.

There are two periods in which corn breeders test combining ability generally called (1) early testing, and (2) testing after practical homozygosity has been reached.

In early testing the inbred is selfed or backcrossed and at the same time crossed to test combining ability. While inbreds that have been selfed for only one to three years are not homozygous for combining ability, such test

TABLE 8

TOTAL CORRELATIONS BETWEEN CHARACTERS OF 110 INBREDS, LABELED 1 TO 12,
AND YIELDING ABILITY OF INBRED-VARIETY CROSSES DESIGNATED AS 15

	Characters correlated											
	2	3	4	5	6	7	8	9	10	11	12	15
1	0.51	0.61	0.48	0.65	0.62	0.55	0.38	0.37	0.22	0.07	-0.06	0.47
2		0.76	0.44	0.48	0.40	0.26	0.19	0.36	0.25	0.08		0.27
3			0.43	0.54	0.50	0.41	0.35	0.33	0.22	0.15	-0.01	0.41
4				0.50	0.44	0.48	0.40	0.29	0.18	0.20	0.08	0.29
5					0.76	0.51	0.60	0.41	0.21	0.15	0.04	0.45
6						0.55	0.74	0.39	0.29	0.19	0.03	0.54
7							0.54	0.24	0.27	0.21	0.15	0.41
8								0.26	0.22	0.20	0.07	0.45
9									0.20	-0.00	0.03	0.19
10										0.35	0.32	0.26
11											0.64	0.25
12												0.28

Multiple value of R for inbred-variety yield and twelve characters of inbred = 0.67

Significant value of r for P of .05 = 0.19.
" " " r " P " .01 = 0.25.

makes it possible to discard low combiners.   Such a
method may rest on a sound genetic basis.   Whether
practically desirable can only be determined from com-
parisons of early testing with testing later after lines are
homozygous.   It has been suggested as a very desirable
method because of the rather common viewpoint that
there was little relation between characters of inbreds
and combining ability.

Richey (1945) has presented an interesting summary
from the work of Jenkins and Brunson that helps to
answer the comparative value of early and later testing
for combining ability.

TABLE 9

COEFFICIENTS OF CORRELATION FOR THE YIELDS OF INBRED PARENTS OR
TOP CROSSES WITH THE MEAN YIELDS OF SINGLE CROSSES
(AFTER RICHEY, AFTER JENKINS AND BRUNSON)

Hybrids correlated with	Previous generations of inbreeding		
	*S_3	S_4	S_6
Inbred parents	.25, .64, .67	.41, .45	
Top crosses	.53	.53	.63, .65, .66, .90, .90

* S_3 = three years selfed, etc.

While for various reasons these r values are not
strictly comparable the yield of inbreds was about as
strongly correlated with mean yield of their single crosses
as the yield of top crosses was correlated with the mean
yield of single crosses.   Correlation values for top cross
yield and mean yields of single crosses were greater in S_6
than in earlier inbred generations.

Singleton and Nelson (1945) recently with sweet corn
have investigated the problem of learning "the earliest
generation of inbreeding in which it is possible and prac-
tical to select for factors for combining ability."   They
conclude, "Even when possible to select for combining
ability in generations earlier than the third, it is probably
inadvisable for two reasons: (1) lines are still segregat-
ing or changing for combining ability, and (2) the diffi-
culty of testing properly a large number of lines in hybrid
combination is so great that it is advisable to inbreed
further and reduce the lines in number before testing."

Earlier studies by Hayes and Johnson (1939) showed that inbreds with good combining ability could be obtained by selecting during the segregating generations for desirable characters followed by testing for combining ability. Similar results have been obtained with inbreds produced by two generations of backcrossing followed by subsequent selection and selfing.

Yield trials of top crosses of the original and of a few selected improved lines are given in Table 10. In these

TABLE 10

Top Crosses of 11 and 14, Inbreds from Minn. No. 13, and of Improved 11's and 14's Obtained by Selection During Two or Three Genera-tions of Backcrossing and During Several Subsequent Generations of Selfing

Inbred	Origin	Per cent M.*	Yield bu.
11	Minn. No. 13	25.2	58.4
A201	(11×23) 11$_2$	25.0	66.7
A204	(11×23) 11$_3$	23.9	62.7
A206	"	29.1	67.6
14	Minn. No. 13	24.7	51.1
A212	(49×14) 14$_2$	23.5	60.8
A215	(14×374) 14$_3$	19.5	48.1

* Per cent. moisture at husking.

studies 11, 14 and 49 are inbred lines of Minn. No. 13 and 23 and 374 are inbred lines of Reid's Yellow Dent. Two or three backcrosses were made and selection was prac-ticed for desirable plant type during the two or three backcross generations and in four or five subsequent gen-erations of selfing. The top crosses were made to Golden King and the yield trials carried out at three locations with three replications per location.

These tests are given to show that it is not too difficult to improve combining ability by this method of breeding and late testing.

Numerous studies in corn have shown the importance of genetic diversity in relation to combining ability. An illustration has been taken from the studies of Andres and Bascialli (1940) in the Argentine (see Table 11). They compared the yielding ability of F_1 crosses between inbreds of three origins as follows: (1) North American inbreds; (2) Argentine inbreds; (3) North American inbreds crossed with Argentine.

TABLE 11

F₁ Hybrids Among Inbreds of Different Origin (after Andres and Bascialli)

Origin	No.	Kilograms per hectare	
		Highest	Average
North America	15	5,155	3,871
Argentine	48	5,566	3,618
N. A. × Arg.	34	5,694	4,317

The importance of genetic diversity of origin is very evident.

After obtaining inbreds with high combining ability they may be used in corn in single crosses, three-way crosses, double crosses, multiple crosses and synthetic varieties. In a study carried out in Minnesota data have been obtained for the yielding ability of 28 single crosses between eight inbred lines that yielded relatively well in all possible single cross combinations. The performance of predicted double crosses was obtained by averaging in each case the yield of four single crosses from the four inbreds used in the double cross, excluding the two single crosses used as parents. The method of predicting the yield of the synthetic variety was described by Hayes, Rinke and Tsiang (1944). The results given in Table 12 include several of the more desirable single crosses compared with two of the more promising predicted double crosses and the predicted yield of the synthetic variety.

The selected single crosses were superior to the doubles when both yield and per cent. moisture were concerned and the selected doubles were superior to the synthetic variety.

TABLE 12

Comparison of Single Crosses, Double Crosses and Synthetic Variety (using 8 Inbreds)

Single crosses	Per cent. M.	Yield bu.
Oh51A × A73	22.1	81.3
Os420 × A73	26.9	88.3
Av. 28 singles	23.5	73.4
Double crosses		
Min. 503	22.8	78.0
" 408	24.2	81.1
Synthetic		70.9
Level sig. 5 per cent.	0.9	3.5

It is apparent from these results and those of Sprague and Jenkins (1943) that under satisfactory environmental conditions, and from the use of the same inbred lines, selected single crosses may be expected to be superior to three-way, double or multiple crosses; that the best three-way has a yield potential somewhat higher than the best double and that the best double has a yield potential higher than the best multiple cross. A synthetic variety produced in Minnesota from the eight inbred lines used in studies of comparative yields of single and double crosses has yielded superior to the open-pollinated variety with which it was compared and is markedly superior in standing ability. It yields less, however, than selected single, three-way or double crosses.

Application to Forage Crop Breeding

From the brief reviews given it is evident that heterosis results from various genetic causes, including (1) partial dominance of linked growth factors, (2) the complementary action of genes all of which are necessary to condition the development of the character, (3) the overcoming of the effect of a homozygous, deleterious recessive factor by the introduction of its dominant allel, which in turn makes possible the full activation of desirable growth factors that may have been inhibited by the deleterious recessive, and (4) the increased stimulus from the heterozygous condition of multiple alleles that may have different physiologic effects.

Combining ability is used by plant breeders to express the relative performance of inbred lines or clones in crosses. It is dependent upon yield factors that lead to heterosis in favorable crosses. The combining ability of inbred lines or clones when crossed with each other is dependent not only on their general combining ability but is greater between crosses of diverse genetic origin than in more closely related material.

In forage crops with perennial habit it seems evident, as Tysdal and Kiesselbach (1944) have suggested, that

the combining ability of clonal lines, with or without previous purposeful inbreeding, may be tested by the so-called polycross method.   If it is possible to select self-sterile clones this will insure that cross pollination is obtained.

After selecting clones that have high general combining ability from the polycross yield trial they may be tested in single cross combinations.   Where feasible to produce, selected single crosses appear to be most desirable if the single cross parents can be selected on the basis of self incompatibility and if the parents are cross compatible with each other.   Single crosses between clones that are heterozygous may be analogous to double crosses in corn. If some method can be devised to insure 100 per cent. cross pollination, double crosses in clones of alfalfa, for example, may be analogous to multiple crosses in corn. It seems difficult, and probably impossible to insure 100 per cent. cross pollination in the production of double crosses in forage crops without utilizing male sterility.

In tomatoes, Rick (1945) has presented evidence that male sterility, conditioned by a single recessive gene, occurs with sufficient mutation frequency so that male sterile types of this nature can be found in most commercial varieties.   Male sterility that may make the use of F_1 hybrids feasible has been reported in other crop plants including onions, sugar beets, and sorghum.   Male sterility has been found also in barley.   Perhaps male sterility can be utilized eventually in forage crops to insure cross pollination.

Synthetic varieties produced by combining clones that have good combining ability in all possible single crosses between the clones have been suggested previously as a desirable method of strain building.   The extent of normal self pollination is of great importance in relation to the building of such synthetic varieties from clones of high combining ability as normal self pollination leads naturally to greater homozygosis in successive generations and thus to a progressive reduction in the degree of heterosis.

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THE PRESENCE OF MULTIPLE STRANDS IN CHROMOSOMES OF ROMALEA (ORTHOPTERA)[1,2]

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THE fact that chromosomes become visibly divided in advance of the mitotic cycle in which the parts are separated is already well established for both plant and animal tissues. The presence of more than the traditional two threads in the prophase and metaphase chromosomes of certain plants has been known for over fifteen years (Sharp, 1929). In somatic divisions of *Tradescantia* (Nebel, 1933, 1939, 1941) and *Lilium* (Goodspeed *et al.*, 1935) the telophase chromosome is described as having four strands. Comparable "precocious" subdivision during meiosis is known to occur in a number of plants: *Tradescantia* (Sax and Humphrey, 1934; Kuwada and Nakamura, 1935), *Gasteria* (Taylor, 1931), *Trillium* (Huskins and Smith, 1932, 1935; Sparrow, 1942), and others (reviewed by Sax and Sax, 1935, and by Kaufmann, 1936). In several animals the chromosomes likewise show advance division: Kaufmann (1934) figures an anaphase split, especially evident in the X chromosomes, during somatic mitoses of giant ganglion cells in *Drosophila melanogaster;* the early telophase chromosome of *Ambystoma tigrinum* is described by Dearing (1934) as a bipartite structure giving rise to two nucleoli; and Hughes-Schrader (1940) states that in meiosis of the male coccid, *Llaveiella,* the metaphase I chromosome is four-parted. The chromosomes of male Tettigidae exhibit a longitudinal split during the telophase and post-telophase stages previous to synapsis (Robertson, 1920). The telophases of somatic mitoses likewise show their

chromosomes to be split before entering the resting stage.
Robertson (1931) describes the anaphase chromosomes
of the secondary spermatocyte of a male of *Paratettix
texanus* (Tettigidae) as already visibly double. This
means that the chromosomes in the sperm are split.
Among the Acrididae at least five cases are known. Mc-
Clung (1927) describes an anaphase split in the last pre-
meiotic division of *Mecostethus* and *Leptysma;* Makino
(1936) finds that in two species of *Podisma* the dyad chro-
mosome at first anaphase consists of two chromatids each
composed of two chromonemata; and Nebel and Ruttle
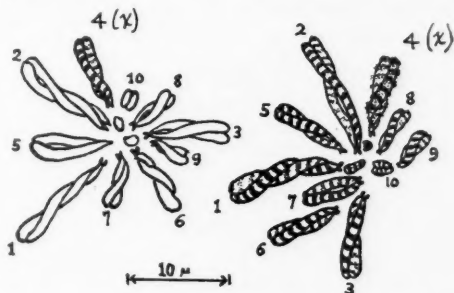(1937) report that in *Dissosteira carolina* during the first

FIG. 1. Camera lucida drawing showing the two daughter haploid groups
of chromosomes during anaphase of the second maturation division in the
male germ cells of *Romalea microptera*. The X chromosome appears in each
group. Each monad is comprised of two twisted chromatids, each of which
shows an internal spiral (drawn in only a part of the figure).

telophase and interkinesis each univalent contains eight
threads and during the second telophase each chromo-
some contains four. The present paper calls attention to
a condition like that in *Podisma* existing in the meiotic
chromosomes of another locust, *Romalea microptera*
(Beauv.), and briefly suggests some implications of multi-
ple chromonemata or polytene chromosomes.

These observations are based upon slides[3] prepared by
the acetocarmine squash method and made permanent by
transferring to 95 per cent. alcohol and mounting in
euparal. Only two drawings are included since a more

detailed account including photomicrographs is being published elsewhere.

Fig. 1 represents daughter groups of chromosomes during late anaphase II of a secondary spermatocyte containing the X chromosome. The coiled chromonemata are indicated in some chromosomes, but in others only outlines of the chromatids (formerly half-chromatids at metaphase) are shown. Homologues are designated by numbers according to relative lengths. The extremely short secondary arm is visible on all but the three smallest of the set of subterminally attached chromosomes. The univalent sex chromosome in Fig. 2 (shown during ana-

FIG. 2.   A single X chromosome (univalent) shown at the dyad stage, *i.e.*, during the anaphase of the first maturation division. Each of the two chromatids is shown to contain two half-chromatids loosely coiled around each other.

phase I) exhibits the typical repulsion of chromatids thus presenting the familiar V configuration (really a double V if the very small secondary arms are considered).

Most important is the fact that each chromatid of the X chromosome is clearly and unmistakably subdivided into half-chromatids which are loosely coiled about each other and which individually show a spiral structure. This condition proves that the half-chromatids are plectonemically coiled since these relational coils are produced when the half-chromatids relax and straighten out partially. Only after the relational coils untwist are the half-chromatids permitted to separate. The precocity of the

X chromosome is borne out by the fact that its four-partite condition is regularly visible at metaphase or early anaphase of the first maturation division. The autosomes, on the other hand, only occasionally show the four-stranded condition before late anaphase or telophase I. The difference is suggested to be due to the matrix which probably allows the X chromosome to relax its coils earlier than the autosomes. The sex chromosome is already fuzzy and relaxing in prometaphase I. A few favorable figures prove, however, that the autosomes likewise contain four threads per dyad. This multiple stranded condition may have far-reaching significance.

The advance splitting leads Sharp (1943) to state that " . . . a chromonema becomes visibly double slightly over one mitotic cycle in advance of the time at which the halves are to separate." He writes further, "There are reasons for believing that the threads are doubled sub-microscopically before any doubleness is seen and, further, that the chromosomes, particularly large ones, may even be more highly compound in terms of visible chromonemata than indicated. . . . " Nebel and Ruttle maintain that the chromatic material visibly divides two divisional cycles ahead of its separation, thus constantly giving the chromosome four threads at all stages except between the first and second maturation divisions, at which time they consider each dyad to be eight-parted. Although in *Romalea* we are able to demonstrate only four visible strands per dyad, this still means that, for this division at least, the chromosomes are divided two cycles in advance. Since the same situation exists in *Llaveiella, Paratettix* and *Podisma* and in many plants it seems likely to be of wide, possibly universal, occurrence.

The structure of Dipteran salivary chromosomes and of other polytene chromosomes in insect tissues has a bearing upon the problem. The longitudinal fibrils which connect the discs in stretched salivary gland chromosomes do not represent individual chromonemata (Painter, 1940, 1941). On the same theoretical basis that the ultimate

gene string must be ultramicroscopic in size, it may be argued that the visible thread in any chromosome, whether in somatic mitosis or in meiosis, can not be a single naked string. Either it must be a thread with sufficient additional substance around it to build it up to visible size (*ca* ¼ micron) or else it must be a large bundle of chromonemata. This latter possibility has many intriguing implications.

If the chromosome can split for two divisions in advance, there is no *a priori* reason why it can not duplicate many times to produce a thread comprised of several hundred gene strings which we assume to be at the molecular level. This is the level of duplication which Sharp calls *elementary doubling*. He distinguishes further between *effective doubling*, at which time "a given agency such as X rays may effect one longitudinal fraction and not another," and *visible doubling*. To these we may add *functional doubling*, which means the differentiation of parts which will separate at the next anaphase movement. Possibly effective doubling and functional doubling occur at the same time but not necessarily so. We have already shown that the visibly quadripartite X chromosome of first meiotic metaphase functions as a unit and that each of its visibly double, descendant monads is functionally single. Obviously the visible split in the chromatids of metaphase I becomes the functional split in the first postmeiotic mitosis (in animals the first cleavage of the zygote, in plants the first somatic division of the male or female gametophyte).

The question arises concerning the mechanism which regulates the separation of threads which themselves are polytene. The explanation is not yet at hand but, if the mechanism functions properly with the quadripartite or eight-parted threads, certainly it may do so with chromosomes more highly subdivided. On the other hand, under special conditions the multiple strands fail to separate, thus creating the highly polytene chromosomes of salivary glands or of nurse cells of certain Dipterans (Bauer,

1938; Painter and Reindorp, 1939). The chromosomes unite into a haploid number of bundles in the latter case but subsequently separate to produce a typical polyploid cell. In at least two very remarkable cases, *Spinacia* (Gentcheff and Gustafsson, 1939) and *Culex* (Berger, 1938, 1941a, 1941b), the polyploid condition resulting from retention of duplicated chromosomes within the same nucleus later return to diploidy through somatic segregation. Thus the mechanism appears to be subject to a wide range of variation, adapting itself to the particular exigency of the cell whether it be for efficient secretion in a gland cell, for rapid multiplication of cells during metamorphosis of insects or during growth of root periblem, for specialized production of germ cells or for just ordinary multiplication of cells in somatic tissues. It is not surprising, therefore, that the mechanism occasionally fails in separating sister chromatids, thus producing polyploid cells such as those previously described in various tissues of *Romalea microptera* (Mickey, 1942, 1945a, 1945b).

Other relationships of multiple stranded-chromosomes, *e.g.,* to mutations, chromosome breaks and genic balance, can not be discussed here but must await publication in a more extended paper.

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THE MEANS OF DISPERSAL OF BATHY-PELAGIC ANIMALS IN THE NORTH AND SOUTH ATLANTIC OCEANS

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In addition to the well-known superficial ocean currents which serve as agencies in the transportation of planktonic organisms throughout the great oceans, there are other currents which are constantly flowing far beneath the surface. The direction of flow of these deeper currents may be at any angle with those in the more superficial water masses in the same geographical region and their populations may be carried in different directions (Sverdrup, Johnson and Fleming, 1942). Living in these deeper currents and in their eddies there are many populations of animals which differ widely from those which are found nearer the surface. In some species, however, the larvae live in the superficial water masses and the adults at lower levels, while in other species the adults migrate between higher and lower levels. Such species become widely dispersed through the oceans.

The more superficial currents, as is well known, carry both animals and photosynthetic organisms, including diatoms, dinoflagellates and other algae which directly or indirectly provide the nourishment for all the animal life of the oceans. The currents and eddies at deeper levels, below the photosynthetic zone, support animals only, and these, as indicated, depend entirely upon such food as may fall or be brought down from higher levels.

By means of these ocean currents a considerable number of species of organisms have attained world-wide distribution. By such means also even sessile organisms have become distributed over vast areas through the

transportation of their free-swimming larval stages gen-
eration after generation (Hesse, Allee and Schmidt,
1937).   But the currents are also responsible for the
destruction of a large proportion of these larvae by carry-
ing them to regions or situations unsuitable for survival.
On the coast of southern California, for example, the pre-
vailing currents are capable of transporting the larvae
of mollusks for a distance of 70 miles or more during
their free-swimming period of about 18 days.

Superficial Ocean Currents

Two of the best-known examples of transport by the
superficial ocean currents are furnished by the larvae of
the American and European eels.   It may be recalled
that the sexually mature individuals, particularly fe-
males, leave their fresh-water lakes and streams in which
they have been living for five to twenty years or more
and migrate to the mouths of rivers and thence to the sea.
There they are joined by males and perhaps by other
females which accompany them far out into the North
Atlantic Ocean.   After journeys varying from several
hundred to three thousand miles or more each species
reaches a different area in the western half of the ocean
north and northeast of the West Indies.   In these areas
the eggs are discharged and fertilized, after which the
young larvae rise to the surface and feed on the plankton.

Although the larvae of the two species become mingled
to some extent, the principal breeding area of the Ameri-
can eel lies somewhat farther west and south than that
of the European species and many of the larvae of the
former species are carried in a westerly direction by the
prevailing surface currents and thence across the Gulf
Stream.   Others are transported to the south and into
the Caribbean Sea and from there to the Gulf of Mexico.
Most of the latter are probably carried through the
Florida Strait and northeast along the western edge of
the Gulf Stream.   At the end of about one year from the
time of hatching, both groups will have become distrib-

uted along the North American coast from Florida to
Labrador. They then transform into ''elvers,'' and most
of these young eels ascend the rivers, the females as a
rule going farther upstream than the males. Much
smaller numbers are carried to the shores of northern
South America, Central America and the Gulf of Mexico
(Schmidt, 1922, 1925).

The surface currents prevailing at the breeding area
of the European eel, however, carry the larvae of that
species toward the eastern edge of the Gulf Stream and
thence to the mid-Atlantic and eastward. After a journey
lasting nearly three years the larvae reach the coasts of
Europe and northern Africa. There, as was mentioned
for the American species, they transform to young eels
and many of them ascend the rivers (Schmidt, 1922, 1925).
The course of the larvae through these long ocean voyages
evidently depends largely upon the prevailing currents in
the superficial water masses, aided by the directive move-
ments of the larvae themselves.

Both the rates of flow and the directions of the ocean
currents, particularly those in the superficial water
masses, are subject to considerable fluctuations from sea-
son to season as the result of changes in winds, barometric
pressure, temperature and salinity. Upwelling of the
deeper water and sinking of the superficial layers are of
common occurrence in certain localities and seasons
(Sverdrup, Johnson and Fleming, 1942). Side eddies
are always present and mixing with the adjacent waters
occurs constantly.

Some of the superficial currents constitute more or less
nearly closed circuits, like those of the Norwegian seas
and the Gulf of Maine, requiring from a few months to a
year to complete the circuit. Other currents, such as the
Gulf Stream, are open systems of vast extent and these
may carry portions of their populations to regions unfav-
orable for existence.

The circulation of water masses through the Gulf of
Maine has been shown by Bigelow (1926, 1927) and Red-

field (1939, 1941) to depend upon a great anti-clockwise cyclonic eddy. This movement carries populations of organisms originating outside the Gulf into the eastern portion of the Gulf and thence along its northern and western sectors. By following the course of a population of the pteropod *Limacina retroversa,* Redfield (1939) concluded that it was transported during the winter for a distance of about 150 miles in four months or at a rate of approximately 1.25 miles per day. This rate corresponds closely with the velocity of movement of characteristic water masses in the same region (Bigelow, 1926, 1927), although in shoal water about the margin of the Gulf the rate may be as much as 7 miles per day.

The reproduction of planktonic organisms may take place in the currents themselves, in the eddies that they produce or in larger masses of relatively stationary water. Evidence has been presented by Sömme (1933) and others that some of these relatively stationary water masses provide the principal reproductive areas for certain planktonic animals. From these endemic areas, portions of the population are carried by currents to other parts of the ocean, the individuals gradually decreasing in numbers as they arrive at less favorable ecological conditions.

Deep Ocean Currents

The deeper ocean currents are naturally less well known than those nearer the surface, but it has been determined that there are slowly moving currents in the intermediate water of the Atlantic basin, at depths usually of 800 to 1,800 meters. Some of these flow in both directions across the equator, while others move in a generally easterly or westerly direction (Fig. 1). Consequently the populations of suspended organisms which are resident in these moving water masses presumably have an equally extensive geographical distribution in so far as changes of temperature and other physical and chemical alterations of the water permit. In these deeper water masses, however, the environmental conditions

remain nearly constant all the way from the subpolar
regions to the equator, although a continuous water mass
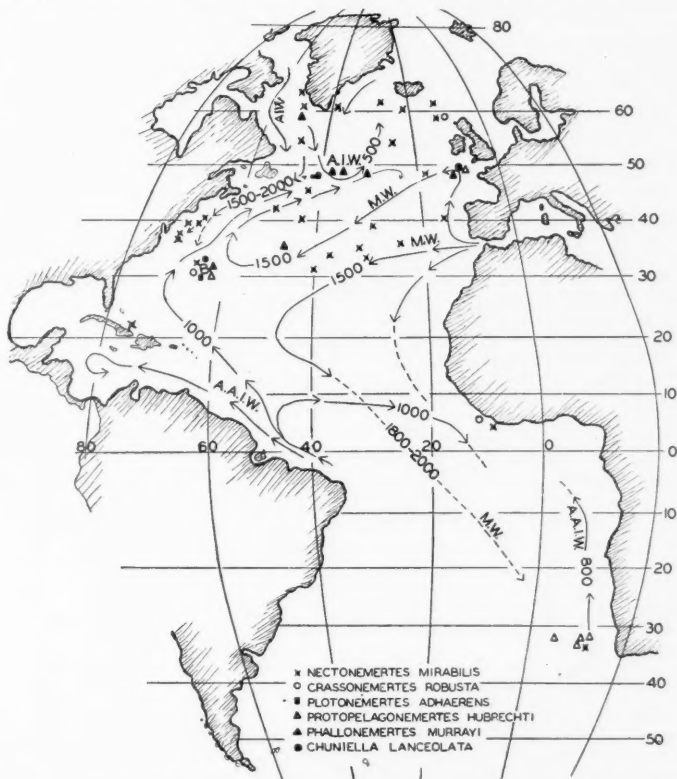

FIG. 1.   Correlation of the distribution, in so far as at present known, of
six of the species of bathypelagic nemerteans found in the Atlantic basin
with the approximate directions of flow of the water masses which they in-
habit.   Numerals indicate average distances in meters from surface at which
the intermediate water masses are flowing.   Broken lines are used for less
well authenticated currents.   Abbreviations indicate: A.I.W, arctic inter-
mediate water; A.A.I.W, antarctic intermediate water; M.W, Mediterranean
water; B, Bermuda area.   (Modified from Sverdrup, Johnson and Fleming,
''The Oceans,'' 1942, with additional data through the courtesy of Dr.
Sverdrup.)

may lie at a higher level in high latitudes than it does
nearer the equatorial region.

Because of the wide extent of these deeper currents, the same species may be found in many regions of the Atlantic basin, from off the coast of Greenland to near the coast of South Africa and from near the coast of Europe to the continental shelf of North America (Fig. 1). Water masses having the same general characteristics are continuous throughout this vast extent of ocean, since these deeper currents are in communication.

In any particular geographical area the various water masses from the surface to the bottom may each carry its
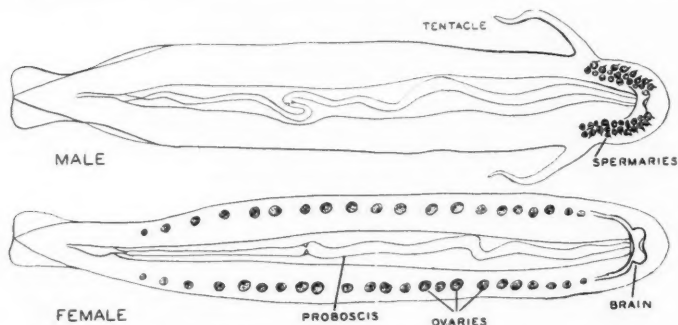

FIG. 2.   Bathypelagic nemertean, *Nectonemertes mirabilis*, male and female, showing horizontally flattened body, with horizontal and caudal fins, tentacles and other adaptations for floating idly or swimming sluggishly in the intermediate depths of the oceans.

characteristic animal populations, since some species or groups have become adapted to one particular type of environment and are, therefore, more or less definitely restricted to it. All members of the tribe *Pelagica* among the nemerteans, for example, live exclusively far beneath the surface of the great oceans, but some of them at deeper levels than others.

These bathypelagic species, as they are called, are highly specialized morphologically and appear to be admirably adapted for existence at considerable depths. In most of them the body is broad and much flattened horizontally, with a large proportion of gelatinous tissue, or parenchyma, and with a relatively feeble musculature

(Fig. 2). Some are provided with a flattened caudal fin, while a few have lateral appendages, or tentacles, which presumably add somewhat to the buoyancy of the body, as well as being of use in holding the two sexes in contact during the mating period (Fig. 2). Other species achieve buoyancy merely by their broad, horizontally flattened bodies, but all individuals are capable of maintaining their position within a particular water mass by the expenditure of a relatively small amount of muscular energy. Although they are well adapted for floating along with the currents, their mobility is sufficient to enable them to move about both within the currents and outside them as far as the environmental conditions will permit.

The water masses in which most of the bathypelagic animals live have temperatures of less than $7°$ C. and as a consequence the viscosity is such as to enable the animals to support themselves with a minimum of muscular effort. It may be recalled that the viscosity of the water is nearly twice as great at $5°$ as it is at $25°$ C. and thereby contributes to the ease of suspension of animals in water of low temperatures.

In the polar regions, where there is relatively little difference between the superficial and deeper water masses in temperature and therefore in viscosity, the depth at which a species may be found is often highly variable. In those parts of the ocean where the superficial layers are much warmer than those at greater depth the populations of invertebrates usually sink to the level at which they can most easily maintain themselves. This often leads to an assortment of sizes or species, with the smallest as a general rule in the surface waters of low viscosity, while larger individuals of the same or different species may be found only in the deeper and colder layers of higher viscosity. But there are many exceptions. Furthermore, fishes and invertebrates with highly developed musculatures may overcome the handicap of an unfavorable viscosity by their own movements.

The Bermuda Area

The portion of the ocean in which the bathypelagic fauna has been investigated most thoroughly is a circular area eight miles in diameter located about nine miles southeast of Nonsuch Island, Bermuda.   During the summers of 1929, 1930 and 1931 the Bermuda Oceanographic Expeditions, under the direction of Dr. William Beebe, drew a total of 1,042 nets one meter in diameter at depths of between 1,000 and 2,000 meters in all directions across this imaginary cylinder of the deep subtropical ocean. The volume of water in this eight-mile cylinder is only one five-millionth that of the total water in the oceans, but from it there were obtained more than 115,000 fishes and large numbers of bathypelagic invertebrates (Beebe, 1937).

The nets were drawn horizontally for periods of usually about four hours after the bottom net had reached the depth of 1,800 meters and then drawn vertically to the surface.   It must be remembered, however, that the nets did not enter exactly the same water in successive years nor even in successive days, for the ocean currents are constantly transporting the water from one portion of the ocean to another.   Through the agency of these currents the constituent planktonic fauna of any particular water mass is being slowly but continually distributed to other geographical areas.

Assuming a more or less continuous flow, the actual volume of water through which the nets passed during the three summers must have been vastly greater than that of an equal cylinder of stationary water.   For the water masses at the locality mentioned during the summer of one year may have been far distant the following summer and the bathypelagic fauna collected on any particular date may have arrived at that locality just in time to be caught by the nets.   It seems quite possible that many of the sexually mature planktonic animals which were obtained may have originated as young individuals some miles distant and that their offspring may live in some other part of the ocean not too far away.

It must not be assumed, however, that these water masses with their suspended faunas are flowing like rivers in a single direction, for oceanographers have determined that the generally onward movement of the water is the resultant of innumerable streams with counter currents and side eddies flowing in all directions. Hence it is not inconceivable that an individual which may have once narrowly escaped the net in the Bermuda area may nevertheless be caught in another net at the same place some weeks or months later, after having made a circuit outside the area in the meantime. It must be remembered, however, that there are also large areas of relatively stationary water in which only eddy movements prevail and in which no distinct currents can be detected.

The region off the coast of Bermuda seems to be particularly favorable for a great variety and abundance of bathypelagic animals because of the admixture of ocean waters derived from several widely separated sources (Sverdrup, Johnson and Fleming, 1942).[2] Such evidence as is at present available indicates that the intermediate ocean water in that region, at depths of 1,000 to 2,000 meters, has a large component of water of subantarctic origin (Fig. 1). This moves in a generally northerly direction at a rate which has been estimated at about one-half centimeter per second or perhaps 400 to 500 meters per day. That would indicate a movement approaching one mile in 4 days. If it could be assumed that such a flow is continuous and at a rate approximating 90 miles per year it would require a period of only 40 to 50 years to bring a population of bathypelagic animals from the South Atlantic to the Bermuda area. From that area some of the members of the population may be carried farther to the north and others deflected toward the east and thence to the middle Atlantic. Other currents may return a portion of the population southward and thence back to the South Atlantic (Fig. 1).

[2] For additional data relative to the movements of these water masses at intermediate depths, the writer is indebted to Dr. H. U. Sverdrup, director of the Scripps Institution of Oceanography.

A second source of the intermediate water off Bermuda
has its origin in the subarctic region of the western At-
lantic (Fig. 1).   This brings, from higher levels in the
north, water which sinks to greater depths off Bermuda.
Consequently it need occasion no surprise to find that the
nemertean *Nectonemertes mirabilis*, which may be found
within 500 meters from the surface in the seas near
Greenland, lives at depths of 1,300 to 1,800 meters or
lower in the Bermuda area.

A third source of water which may mingle with the
flows from north and south already mentioned, is the
Mediterranean outflow (Fig. 1).   Although there are no
bathypelagic nemerteans in the Mediterranean Sea, the
populations in the eastern and central North Atlantic may
be brought into the currents of mixed water as they flow
from east to west through the central North Atlantic.

Hence, it may be expected that populations from any
of these and perhaps from other far distant sources may
be found drifting past the Bermuda area in one direction
or another whenever a net is lowered to the depth at which
each species finds the conditions for survival and repro-
duction most favorable.   But the populations encount-
ered may differ from month to month or even from day
to day.   Certain species, however, appear to be pres-
ent at all times, not only in the Bermuda area but also
throughout the North Atlantic and in some parts of the
South Atlantic.   The bathypelagic nemertean *Necto-
nemertes mirabilis* is an example of such a species, since
it has already been found in the South Atlantic west of
South Africa, in the equatorial Atlantic, near the West
Indies, off the eastern coast of North America, through
the width of the North Atlantic to near the coast of Spain
and northward to the latitude of southern Greenland.
This indicates a range of nearly 100 degrees of latitude,
from 34° S. Lat. to 64° N. Lat. (Fig. 1).   Hence it is obvi-
ous that no matter what may be the direction of the flow
at the time of the collection or from whence the water may
have come, that species may always be expected either
in the net or in the vicinity.

The nemerteans, as mentioned, float along with the current or are carried into eddies, with only feeble muscular movements. The fishes, on the contrary, are capable of relatively rapid locomotion and in paths having little, if any, relation to the direction of the currents. Consequently certain species, particularly those that have a tendency to collect in groups or swim in schools, may remain indefinitely in any favorable locality. Beebe (1937) obtained in this same area during three summers a total of 115,747 specimens of abyssal fishes, including 220 species or more than one third of all the species of deep-sea fishes then known to science. The evidence indicates that these represented stable populations, since he caught 1,047 individuals of *Myctophum laternatum* in 1929, 877 in 1930 and 905 in 1931, while in the same years the same nets caught only 4, 2 and 2 specimens of *M. fibulatum*. One species was represented by 57,512 specimens, while only a single individual of each of 54 species was obtained.

These nets also caught more than 10,000 specimens of caridean decapod crustaceans, including 36 species (Chace, 1940). Most of them were taken below 1,000 meters. Two of the species were represented by 4,572 and 1,947 individuals, respectively, while only a single specimen of each of seven species was obtained. It is of interest to note that 15 of the 25 previously described species have also been found in the Indian Ocean, 11 in the equatorial Atlantic, 11 in the eastern North Atlantic, 6 off the Cape of Good Hope, 9 in the western Pacific, 6 in the eastern Pacific, 5 off the coasts of Ireland, 5 near the Hawaiian Islands and 4 in the southern Pacific.

Chace emphasizes the importance of ocean currents, as well as the temperature and chemical composition of the water, in the distribution of these crustaceans throughout the relatively low latitudes of all the oceans. The deep-water currents indicated in Fig. 1 may suggest the means of distribution of the species through the North and South Atlantic and it may be assumed as probable that these

currents are in communication with those in the other oceans. The problem of distribution is complicated by the tendency of some of the species to migrate up and down between lower and higher levels and thereby between the deeper and more superficial currents if such are present in their localities. This tendency would naturally facilitate the widest possible dispersal by passive transportation.

In addition to the 115,000 fishes and 10,000 caridean crustaceans mentioned above, the same nets also obtained more than 1,200 specimens of amphipod crustaceans (Shoemaker, 1945). These represented 98 species, there being but a single representative of each of 28 species and 360 representatives of one other species. Some of them have a depth range from the surface to 1,800 meters or more and consequently are of world-wide distribution.

As compared with the numbers of fishes and crustaceans, the bathypelagic nemerteans found in the Bermuda area were very few, consisting of a total of only 105 individuals representing 12 genera and 14 species (Coe, 1945). Several of them are of unusual interest, however, as examples of wide transportation by the deep ocean currents. Eight of these 14 species have not yet been discovered elsewhere, three will be mentioned as occurring in both the North and South Atlantic, while the other three are at present known only from the North Atlantic (Fig. 1). The distribution of *Nectonemertes mirabilis* in so far as at present known has been mentioned already and is indicated in Fig. 1. Another species, *Plotonemertes adhaerens*, seems to find the mixed waters of the Bermuda area particularly favorable for reproduction, since a total of 35 representatives of this species has been obtained in that area, while only a single specimen has as yet been found in all the rest of the oceans. It is possible, however, that the nets used elsewhere were not lowered to the appropriate depth, for this species lives near the lowest limits reached by any of the nets in the Bermuda area. The single specimen known

from the middle North Atlantic was likewise taken in the lowest of several nets.

Protopelagonemertes hubrechti has likewise been found in the South Atlantic west of South Africa, in the Bermuda area and in the eastern North Atlantic southwest of Ireland. *Crassonemertes robusta* has been reported from the equatorial Atlantic (7° N. Lat.) near the coast of Africa, in the Bermuda area and northwest of Great Britain (58° N. Lat.). The three species that have been mentioned are the only bathypelagic nemerteans that have as yet been found both in the tropical or South Atlantic and in the Bermuda area, but it must be remembered that up to the present time relatively few samples of the bathypelagic fauna of the Atlantic between 30° S. Lat. and 30° N. Lat. have been obtained.

Another nemertean with a wide geographical range is *Pelagonemertes rollestoni*. This species occurs throughout the entire width of the South Atlantic and it has also been collected in the northern part of the Indian Ocean, as well as far south of Australia. This range covers nearly 180 degrees of longitude and about 55 degrees of latitude. The great differences in surface temperatures at these far distant regions presumably have little influence on the natural habitat of these worms so far beneath the surface.

Only two individuals of *Chuniella lanceolata* are known at present. One of these was found in the Bermuda area and the other in the North Atlantic southwest of Ireland. The former specimen was caught at a depth of about 1,600 meters and the latter at 1,000 meters.

If the collected specimens have been correctly identified, another species with a wide geographical distribution is *Dinonemertes investigatoris*, for the type specimen came from the northern Indian Ocean, while two other representatives were taken in the central and northern North Atlantic. Even if it could be assumed that a single population of this species extends at the present time throughout the range indicated, such a population

would find essentially uniform conditions in its normal habitat at depths between 1,000 and 2,000 meters in all parts of this wide expanse of oceans. *Nectonemertes minima* has been taken at various localities in the eastern Atlantic oceans, from a point northwest of Ireland, across the equator to near the Cape of Good Hope. This represents a distance of 92 degrees of latitude (57° N. to 35° S.).

The fact that in the Bermuda area only a single specimen of each of so many species of fishes and invertebrates was obtained in a total of more than 600 hauls from nets which had been drawn for four hours at the depth at which that specimen was found would seem to indicate very sparse populations at those levels and at those times. However, with drifting populations which may be carried in various directions throughout the vast expanse of the North and South Atlantic oceans, the chances of catching with a one-meter net even a single representative of a species composed of millions of individuals must be very small. If the individuals have a tendency to collect in widely separated groups, as would be expected in unisexual species, the chances of the net reaching one of the groups would be even smaller.

It was mentioned previously that only 42 species of bathypelagic nemerteans have as yet been collected in the North and South Atlantic oceans. For most of these the populations would also appear to be very small in the regions where the collections were made, since only a single representative of each of 18 of the species has been caught. Of the other 24 species, 8 are known from two specimens each, 5 from three specimens each, and 11 from four or more specimens each.

Only one species, *Nectonemertes mirabilis,* appears to be both abundant and widely dispersed, for at least 170 representatives have been caught, of which 44 were taken in the Bermuda area. It was mentioned also that 35 specimens of *Plotonemertes adhaerens* were caught in the

same area and only one in all the rest of the oceans. This may be considered as evidence of localized areas of relatively high reproduction. From these areas, which may be only temporary, portions of the population may be carried by currents to far distant regions where other colonies may be established after the reproduction of many generations on the way.

Both the species mentioned in the preceding paragraph have structural adaptations by means of which the two sexes can cling together and a certain degree of gregariousness among the members of each species may be assumed. All are of separate sexes and some have special adaptations for internal fertilization. For most of the species, survival would obviously be impossible if the populations were actually as sparse as the collections would indicate. It must, therefore, be assumed that there are other regions or greater depths at which a denser population may exist, or that by chance the nets have missed such groups as may have existed in the vicinity.

And this is equally probable as regards the other groups of the bathypelagic fauna. Many of the species of fishes and crustaceans were mentioned on the preceding pages as being represented in the Bermuda collections by only a single specimen. In not a few cases that specimen is the only discovered representative of the species. Nevertheless, at the low temperatures prevailing at the depths where these species are found, the rates of metabolism are presumably lower than at higher temperatures and the normal span of life relatively long. Consequently the two sexes in even sparse populations would seem to have a greater chance of meeting at the reproductive period than would be the case under other conditions.

The influence of eddies and larger areas of relatively stationary water may be of great importance in the localization of the populations and it is not improbable that there are some regions where a species could remain within a more or less closely circumscribed area indefinitely, as explained by Sömme (1933). From such en-

demic areas representatives of the species might be car-
ried to distant parts of the oceans, reproducing successive
generations on the way as long as the ecological condi-
tions remain favorable.   It seems quite possible that for
certain species the region about Bermuda may represent
such an area.   There are, moreover, large portions of the
oceans, including the Sargasso Sea, in which there is rela-
tively little lateral movement of the water at the depths
inhabited by the bathypelagic fauna.

It might be expected that the members of this fauna
would multiply most rapidly near those regions where
the phytoplankton is most abundant because, as has been
stated, they depend directly or indirectly upon food which
comes down from the photosynthetic zone near the sur-
face.   Since the reports indicate that neither in the Ber-
muda area nor in the Sargasso Sea is there a conspicuous
abundance of phytoplankton, it has sometimes been as-
sumed that such conditions are indicative of a low rate
of production of the phytoplanktonic organisms.   It is
quite as probable however that a high rate of reproduc-
tion may be associated with an equally high rate of con-
sumption by grazing animals and that much food is actu-
ally produced.   Furthermore, the food materials are also
widely distributed by the ocean currents and can be
brought into less prolific areas.

As a consequence of this wide circulation of the ocean
waters it seems quite possible that representatives of all
the bathypelagic fauna inhabiting any part of the North
or South Atlantic may from time to time or eventually
drift through the Bermuda area.   It seems highly im-
probable, however, that the populations are distributed
uniformly over the wide expanse of the oceans between
any two or more localities where their representatives
have been found.   Nor should a species be thought to be
restricted to a closely limited area simply because it has
been taken at only a single locality.   It seems more proba-
ble that the populations are associated in groups which
drift about in the currents or collect in eddies or larger

masses of relatively stationary water generation after generation as long as the regions or depths to which they are carried offer conditions favorable for existence.   By affording such opportunities for passive transportation, the currents supplement, but they do not supersede, the dispersal of oceanic populations by random individual migrations.

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CINEMATOGRAPHY AND THE STUDY OF CHILD DEVELOPMENT[1]

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DURING the last twenty years, the Clinic of Child Development at Yale University has been using the motion picture camera as a basic research tool. As early as 1924 the Pathé Review had made a cinema record of the work of the clinic in a film entitled: "The Mental Growth of the Preschool Child." The sizzling arc light did not unduly disturb the infants or the record. The film depicted stages of psychological development from birth to six years of age, and served to demonstrate the potentialities of cinematography.

We soon embarked on a systematic program which led to a charting of the ontogenesis of child behavior during the first five years of life, with special concentration on the period of infancy. The cinema is an ideal instrument for the investigation of behavior patterns because it captures the behavior in its totality; it "sees" the whole field of behavior with equally distributed vision. And the film remembers infallibly; it registers simultaneously the attitudes of the head, trunk, arms, legs, eyes, fingers and face. It crystallizes any given moment of behavior in its entirety. By multiplying these moments, cinematography reconstitutes the movements of a whole episode of behavior. But in the service of genetic research the cinema can also make records of succeeding days, months or years, and bring them into seriation. Thus the cinema makes available for study (a) the behavior moment, (b) the behavior episode and (c) the developmental cycle.

The cinema furthermore enables us to dissect a behavior pattern and to construe it morphologically; that is, in terms of form relationships measured in time and space. Indeed, when any given behavior pattern is once

[1] Written by request for THE AMERICAN NATURALIST.

captured by the cinema film, it becomes as tangible as tissue.   The *cinema lucida* permits us, so to speak, to bring the behavior of the infants into the laboratory in a dissection tray for analytic study.   One of several versions of an analytic viewer is pictured herewith.   Cinemanalysis is an objective method of behavior research which enables us to approach the problems of mental growth from the standpoint of *developmental morphology*.   Problems of human individuality and culture must be approached from the same standpoint.

The Photographic Research Library of the Clinic has assembled several hundred thousand feet of systematic cinema records of the behavior development both of normal and atypical infants.   Most of the records were made at lunar month intervals under controlled and also under naturalistic conditions.   The films have been classified and catalogued by library methods and can be consulted chapter and verse.

These films have provided the source material for reconstructing the ontogenetic course of infant development.   The records are codified in "An Atlas of Infant Behavior" in two volumes illustrated with 3,200 action photographs, which delineate the forms and growth of human behavior patterns:

> I. *Normative Series*.   This volume portrays the growth of posture, locomotion, prehension and adaptive behavior at lunar month intervals from birth through 56 weeks of age.   The normal infant's characteristic reactions in 25 different behavior situations are depicted in successive chronophotographs enlarged from individual cinema frames.   Time values and detailed accompanying text reconstruct the behavior patterns in dynamic sequence for objective, analytic study.   The infants were photographed nude to increase the scientific values of the delineations.
>
> II. *Naturalistic Series*.   This volume portrays the behavior of similar normal infants in their cultural environment under the natural conditions of domestic life: feeding, bath, play, sleep, parent-child relationships and social situations involving other children and adults.

In addition, the photographic research library contains extensive cinema records of the behavior characteristics

of infants and children with clinical defects and devia-
tions (amentia, endocrine disorders, cerebral injuries,
prematurity, sensory deficiencies, etc.).

Charles Darwin's work on "The Expression of Emo-
tions in Man and Animals" is a classic example of a
naturalist's insight into the biological aspects of human
behavior.   He used photographs not only to embellish
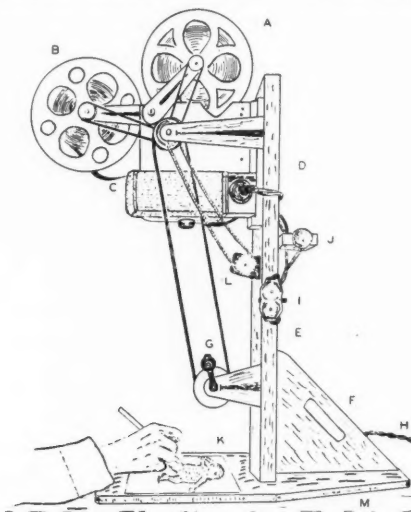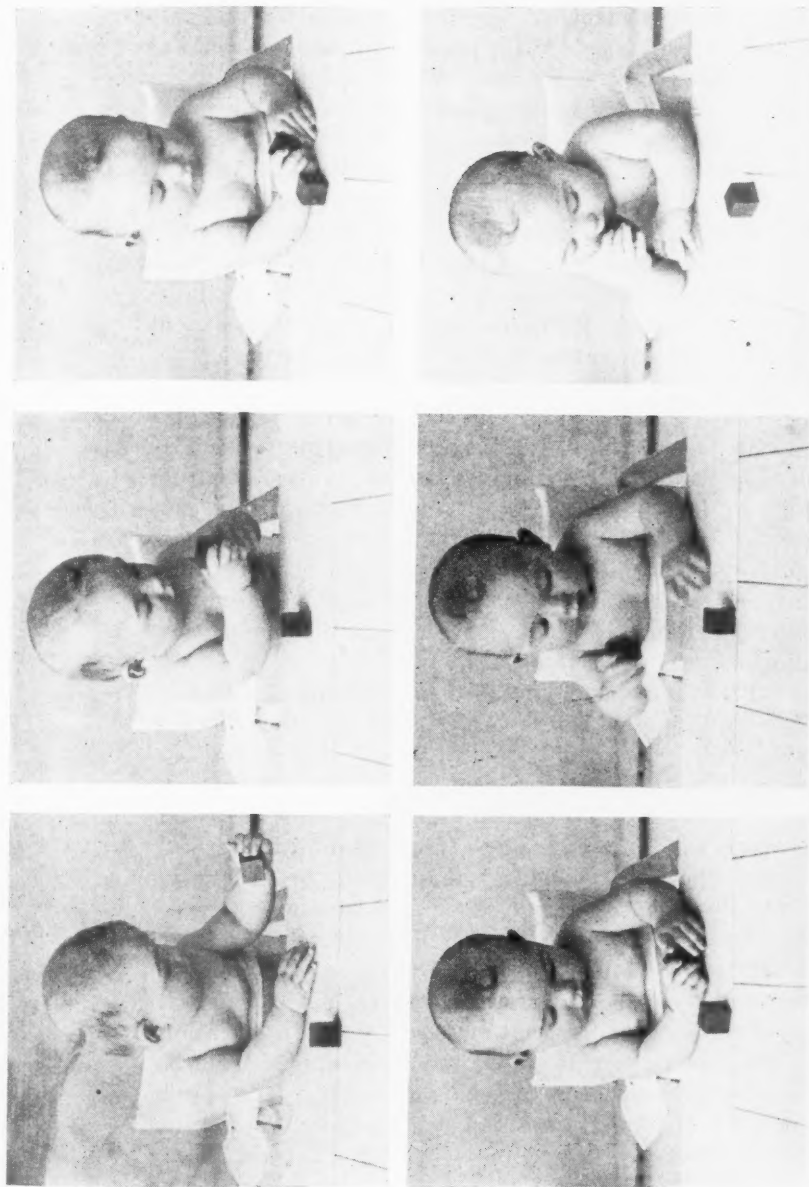his text, but as an aid to study, remarking, "I found

FIG. 1.   Analytic viewer used in the cinemanalysis of infant behavior
patterns.

photographs made by the instantaneous process the best
means of observation, as allowing more deliberation."

Cinemanalysis is a method of observation which per-
mits us to examine the successive phases of motion with
complete deliberation.   The simplest device for accom-
plishing this analysis is an ordinary projector, mounted
on a portable vertical stand which rests on a desk or table,
as pictured in the accompanying illustration.   The pro-
jector is operated by a small handcrank and throws an
image 4 by 5 inches in size upon a white enamel plate.

FIG. 2. Six pattern phases of an episode of cube behavior, identified by cinemanalysis. The infant is 24 weeks old ; the phases are reckoned from 0 to 36 seconds.

24 WEEKS - 4 - 14 - .17.5 - 18 - 20.5 - 36 Secs.

The operator controls the successive images by means of the crank. He employs the analytic viewer in much the same way that he would use a microscope for histologic study. In one case he examines a specimen of tissue; in the other, a specimen of behavior.

Cinemanalysis, therefore, is extremely simple in principle. It is nothing more or less than an objective method for observing the forms of behavior patterns by alternately stilling and animating the cinematic images. This method lends itself to self-instruction, and fosters independent insight. By controlling the crank, the student comes to intimate grips with the dynamic morphology of behavior. If need be, he can witness a given behavior pattern time and again, selecting different aspects for repeated observation. The flexibility and juxtaposability of film materials also facilitates comparative study of varying levels of maturity. This type of study is particularly valuable to the clinical student interested in the norms and deviations of child development. The self-instruction films are regularly used in our clinic in the training of medical externes in methods of developmental diagnosis.

Edited films also have value for mass instruction. The photographic research library of the clinic has furnished the source material for a series of educational sound films (with spoken commentary by the director), now distributed by Encyclopedia Britannica Films Incorporated, Chicago. These films deal with the early stages of child development and are supported by a variety of monographs and books concerned with the psychology and care of the infant. More recently The March of Time has made a full-length documentary sound film of the developmental research of the Yale Clinic with special reference to social implications and applications.

The cinema proves to be a unique medium for clarifying the elusive process of behavior growth. The psychological individual is an action system,—a complex system which changes with age, and which has a natural history.

Behavior grows, and as it grows it assumes characteristic forms.   The study of early human behavior, therefore, is not unlike the study of developmental anatomy.   Although cinematography, in itself, bakes us no bread, it makes the elusive data of behavior growth more accessible to scientific investigation.

OBITUARY

FRANK MICHLER CHAPMAN

JOHN T. ZIMMER

AMERICAN MUSEUM OF NATURAL HISTORY

FRANK MICHLER CHAPMAN was born in Englewood, New Jersey, on June 12, 1864, the son of Lebbeus Chapman, Jr., and Mary Augusta (Parkhurst) Chapman. He graduated from Englewood Academy in 1880 and entered the American Exchange National Bank of New York City, apparently destined for a career in the banking profession.

His interest in birds had already been awakened, but his banking duties gave him little time or opportunity to devote to them, although he spent his holidays and week-ends in various related activities.

He had already collaborated with the U. S. Bureau of Biological Survey in taking counts of local birds, had tried his hand at taxidermy, and had met a number of other bird students, professional and amateur, with some of whom he was to be more closely associated in future years, and forces were undoubtedly at work within him that were to affect his whole future life. Eventually, in 1886, these forces prevailed and he resigned his position in the bank to devote his entire time to birds.

He spent his first winter as an independent investigator in Florida and returned to New York with a collection of birds he had secured during the season's work. He obtained permission from the American Museum of Natural History to take his birds there for comparison with the museum's collections, and remained for the rest of the summer working for George Sennett, an independent ornithologist interested in the birds of Texas, and as a volunteer assistant to Dr. J. A. Allen, head of the Department of Mammals and Birds. In this brief period he gained his introduction to museum activities and to the world of foreign birds as represented in the American Museum's series.

The following winter he returned to Florida and resumed his field work, making the acquaintance of Charles B. Cory, with whom he planned a joint local exploring expedition. Before the expedition set out, however, he received an offer to join the staff of the American Museum as Dr. Allen's assistant, and dropped all other plans to take advantage of the new and welcome opportunity.

Thus, on March 1, 1888, he began his official connection with

the museum which he served so long and faithfully for over half
a century.   He was made assistant curator of the joint Depart-
ment of Mammals and Birds in that year, associate curator in

FRANK MICHLER CHAPMAN

1901 and curator in charge of birds in 1908, and in 1920, when
the Department of Birds was formally separated, he was made
its first curator, a position which he held until his retirement in
1942.

Upon reaching the museum in 1888, he began at once to make the most of his opportunities. The systematic exhibit of birds was broken up into regional sections to give a more concise picture of the bird life of the different parts of the world. A special exhibit was prepared of the birds of the local New York City region, with a section devoted to the "Birds of the Month" that was regularly changed to keep pace with the monthly alteration in the calendar of nature. This monthly series is still maintained in the museum halls.

At this time, also, he gave his attention to the important concept of the "habitat group" which he developed and expanded into a major project. There had been earlier habitat groups in various museums, but they left much to be desired. Mr. John L. Cadwalader of New York City offered to underwrite an attempt at improvement. Chapman accepted the challenge and produced the Cobb's Island Group of shore and water birds, with natural foreground and painted background, that set a new mark in exhibition work. It was so successful that he was empowered by the museum to furnish an entire hall of similar groups of North American birds—a task that occupied his time for the next ten years and carried him widely over the North American continent. The completed Hall of North American Birds still stands as a monument to his industry and vision. His interesting book, "Camps and Cruises of an Ornithologist" (1908) describes his experiences in obtaining the material for the twenty-nine exhibits that, with one later addition, comprise this historical series.

The museum halls afforded only one means of reaching the public to whom Chapman was forever carrying the appeal of the bird in nature. The lecture platform and the medium of books and magazine articles furnished other outlets. His popular writings enabled him to reach a far wider circle than that embraced by museum visitors, and in these other fields he was equally successful. One of his earliest tasks was the preparation of his "Handbook of Birds of Eastern North America" (1895) that has since gone through numerous editions and two revisions and still remains a standard work of undiminished utility. His "Bird Life" (1897), "Bird Studies with a Camera" (1900), "Color Key to North American Birds" (1903), "The Warblers of North America" (1907), and several lesser books are outstanding examples of his efforts to bring the birds to the people.

The growth of the Audubon Society, established a few years

earlier by George Bird Grinnell, gave still another opportunity for public service. Realizing the need for a magazine in which young observers could publish their observations and which would also serve to guide them in their studies, Chapman obtained from the society its assurance of support and, in 1899, began the publication of *Bird-Lore* as its official organ. This highly successful journal he continued to edit until the close of 1934, when it was taken over by the organization, now the National Audubon Society, and continued, though with subsequent (1941) alteration in title to *The Audubon Magazine*. Throughout the thirty-six annual volumes that were issued under Chapman's able editorship there are numerous articles of his own among which the regular page of editorial comment in each number must not be overlooked.

In such wise he played his outstanding rôle as a popularizer of bird study, in which he was preeminent. How many bird students, from casual observers and makers of "bird lists" to professional ornithologists, owe to him their early inspiration, it is impossible to estimate, but the number is unquestionably large. And yet he confessed that his standard advice to young people who came to him for counsel was not to adopt ornithology as a vocation—not that he lacked faith in his own chosen profession but because he believed that if the neophyte had the true inner fire he would go on in spite of such discouragement, but if he lacked it he would be likely to prosper more in some other field.

Chapman declared himself to be primarily a field ornithologist, interested in the living bird in relation to its environment, and there is a wealth of evidence in his writings to support this contention. It was the songs of the birds that first drew his boyhood attention to them and his ear was always attuned to their music. He often referred to birds as "Nature's most eloquent expression."

Nevertheless, as a museum curator, he necessarily devoted a great deal of his attention through the years to the study of specimens, although he still maintained that his ultimate object was the same—to determine the bird's place in nature. A long list of scientific papers exists to his credit to attest his activity in this branch of ornithology. He became interested at an early date in South America—probably because of the collections that were at hand when he came to the American Museum—and his technical papers deal largely with the birds of that area. His final summations of his studies of specimens were, however, philosophical

discussions of distribution and evolution rather than simple catalogues of species and specimens, as is amply demonstrated by his important "Distribution of Bird Life in Colombia" (1917) and "Distribution of Bird Life in Ecuador" (1926).

In these two books, as in other writings, Chapman developed his theories as to the origin and distribution of Andean birds with particular emphasis on vertical life zones and their interrelationship. His conclusions on this subject have been of far-reaching importance and have formed the basis for many subsequent discussions of similar problems. In the course of these studies much taxonomic work was accomplished and there are many new forms of birds that bear Chapman's name as author as well as many that have been named in his honor by other workers.

To get material for these investigations, Chapman visited various parts of South America at different times and thus secured first-hand knowledge of the terrain and the birds about which he was writing. At the same time he was concerned in building up the museum's world-wide collection from other sources, enlisting the support of many friends of the institution, among whom Dr. Leonard C. Sanford, of New Haven, Connecticut, must ever be listed at the head. The climax was reached in 1932 when the great Rothschild Collection at Tring, England, was added to the museum's series through the generosity of the heirs of Harry Payne Whitney of New York City.

In more recent years, Dr. Chapman chose to spend his winters on Barro Colorado Island, in the Canal Zone, where the study of tropical birds and other animals could be pursued under the most favorable conditions. Two books, "My Tropical Air Castle" (1929) and "Life in an Air Castle" (1938), record many of the observations made during these periods, while various special reports discuss particular problems in greater detail.

During the First World War, Dr. Chapman served with the Red Cross, first as director of the Department of Publications and later as a special commissioner to Latin America. At the close of the war, two years later, he returned to New York and resumed his museum activities, which he continued until his retirement on July 1, 1942. Shortly thereafter he removed to Florida where the milder climate gave him the opportunity for year-round outdoor studies. There he remained until early in 1945, when he came north for the summer. Serious illness required his entrance into St. Luke's Hospital in New York City, where he died on November 15, 1945. His wife, Fannie Bates

(Embury) Chapman, whom he had married in 1898, died in September the preceding year.   His son, Major Frank M. Chapman, Jr., U. S. M. C., survives him.

For his scientific attainments, Dr. Chapman was honored by many organizations and institutions.   In 1913, Brown University conferred on him the degree of doctor of science.   He was the recipient of the first Elliot Medal, the Brewster Medal, the John Burroughs Medal, the Roosevelt Medal and the first Linnaean Society Medal.   He was an honorary member of the British Ornithologists' Union, the Deutsche Ornithologische Gesellschaft, the Club van Nederlandsche Vogelkunde, the Sociedad Ornitológica del Plata, the New York Zoological Society and the Explorers' Club; fellow and past-president of the American Ornithologists' Union and one-time assistant editor of *The Auk;* member of the National Academy of Sciences, the American Philosophical Society, the Biological Society of Washington, the American Society of Naturalists, the New York Academy of Sciences, the Century Club (New York) and the Cosmos Club (Washington) ; and member and past-president of the Linnaean Society and the John Burroughs Memorial Association.

Dr. Chapman's own story, "The Autobiography of a Bird-lover" (1933) is filled with details of his abundant career that have been only briefly sketched here.   He was a wise and kindly mentor, ever willing to give the benefit of his experience to those who asked for it.   His name is firmly established on the records of North and South American ornithology where it will remain for all time.   He will be equally remembered as the foremost apostle of popular bird study in his time—a time of which Elliott Coues wrote in another connection (*Bird-Lore*, 3: 13, 1901) that there was "—one of the most remarkable growths of the humanitarian side of ornithology that has ever been witnessed in the history of science."   A large part of this growth may be ascribed to Dr. Chapman's influence.   As Lord Grey of Falloden said of him on the occasion of a lecture on Darwin's Chile that he delivered before the Royal Geographical Society on May 31, 1926: "—he is one of those in whom knowledge quickens feeling, and that quickening of feeling gives a special gift of imparting the knowledge which he acquires to others; and that sense of enjoyment which he conveys of the knowledge which he has acquired is an incentive to others to acquire it too."

REVIEWS AND COMMENTS

Vertebrate Paleontology. Second Edition. By ALFRED SHER-
WOOD ROMER. Chicago: University of Chicago Press, 1945:
i–ix, 1–687. $7.50.

COMPLETELY rewritten and brought up-to-date, this
standard treatise is now rendered even more valuable
than before, not only as a text-book but also as a reference
work by which vertebrate zoologists and students of
evolution may readily avail themselves of the vitally
significant data of vertebrate paleontology. Particularly
important additions are the three chapters that present a
chronological summary of the phylogeny of the verte-
brates. The outline classification of the Vertebrata is
very usefully expanded to include a comprehensive list of
genera known as fossils. From a pedagogic viewpoint
the rather extensive taxonomically arranged bibliog-
raphy is perhaps the logical way to present references,
though more serious students would much prefer a de-
tailed documentation of the text. The index is compre-
hensive, but only for systematic items.

In contrast with the thorough and detailed treatment
of some groups, particularly the fossil reptiles and mam-
mals, the introductory chapter is rather glaringly elemen-
tary and nontechnical, certainly designed to frighten no
one. It provides a very limited background of evolu-
tionary theories and phenomena, of taxonomy and classi-
fication, and of the structure, ancestry and general classi-
fication of the vertebrates. Nor are these subjects further
discussed as separate topics. It is to be urged that in
preparing a third edition the able author will add at least

one chapter that will bring the data of his subject to bear on the principles of general systematics and evolution.

Certainly all users of the book would profit from an adequate presentation of the phylogenetic concepts that are particularly those of the paleontologist. In the current edition the contrast between vertical and horizontal classifications is not only overly simplified but also, I think, actually misleading. On the same family tree the division between groups is drawn for a theoretical horizontal classification only slightly higher on the two main branches than it is for a vertical classification. Neither scheme is unnatural in the sense of polyphylety, whereas the essence of the horizontal scheme, as I understand it, is that the division between groups cuts across two or more phyletic lines that are developing similarly and simultaneously, although along independent phyletic lines. Romer so uses the term and concept of horizontal classification in dealing with the group ''Subholostei,'' which appears to represent similar stages in fish phylogeny that were attained at about the same time along several not immediately related lines. The same concept could have been introduced even more emphatically in treating (or in disposing of) the ''Mesichthyes''—an almost certainly unnatural assemblage of fish groups each of which has attained one or another of the progressive characteristics of the more advanced teleosts. Such attainments appear to have been preordained, but more probably represented the same advantageous adaptations separately evolved.

There is a valuable discussion of the primitive jawless vertebrates (Agnatha), based on the very illuminating researches of recent years. Particularly pleasing is the reserve shown toward the inherently improbable though usual view of paleontologists that the heavily mailed Paleozoic fishes are the direct ancestors of the later fishes and the indirect precursors of the tetrapods. That the great majority of well-known Paleozoic fishes were thickly armored can be explained on two bases: (1) they were more readily and more perfectly fossilized because of

their armor and because they were bottom dwellers; (2) most of the fishes were forced into the adaptation of a protective covering by such predators as water scorpions. Other fishes of the same age were doubtless more generalized. Some presumably received adequate immunity from attack by swimming more rapidly at the surface. The Anaspida and some Heterostraci had body form and fin structure which by mechanical reasoning and by comparison with living fishes of known habits lead one to infer that they swam against the surface film and leaped out of the water when attacked. This idea seems to have escaped the paleontologists.

The author's views that cartilage is a larval specialization and that bone was the antecedent structure are given special emphasis. These ideas do have a ring of truth, but I would prefer the view that bones and denticles were both basal developments. On this view some groups specialized in bone and developed an armor of bony plates while the denticles degenerated or became fused with the skeleton, whereas other groups retained strong denticles while their bony structure weakened and became replaced by cartilage.

In regard to the taxonomy of fishes Romer, like almost every inquirer, is bewildered by the variety and complexity of the classifications of recent ichthyologists, particularly Jordan and Berg. In striving to effect a compromise between these and older views Romer arrived at a scheme that is not uniformly happy. Perhaps the greatest need in vertebrate zoology is for a thorough revision of the classification of fishes.

Though intended as constructive these criticisms on re-reading seem ingracious as well as overly specialized. Romer is not an ichthyologist and his treatment of the tetrapods seems to be much more adequate than that of the fishes, and there is much to be commended in the chapters on Pisces. He has bettered an already valuable treatise, which covers a very important branch of zoology more satisfactorily than does any other book.

An Introduction to Physical Anthropology. By M. F. ASHLEY MONTAGU. Springfield, Illinois: Charles C Thomas, 1945, i–xiv, 1–325, figs. 1–25. $4.00.

REPEATEDLY the author of this book cuts into the limited space at his disposal to continue his attack on "race" concepts. With seemingly religious fervor he stresses the view that all human races are equal in mental endowment. The unity of man is his text. In his brief, unillustrated account of the types of modern man he minimizes the recognized racial distinctions. He even holds that most races are mere abstractions. The very word "race" is anathema, either to be written within quotation marks or discarded in favor of "division" and "ethnic groups" (collectively "varieties"). Perverted Nazi ideas and the nearly forgotten folklore of "blood" are introduced to the disparagement of race concepts.

Inconsistencies mark the discussions of race. Montagu admits that the genetic differences between individuals in mental qualities are as great as in physical characters and regards "ethnic groups" as being characterized by different gene frequencies, yet denies the obvious corollary, that races are significantly different in brain functions.

Repeatedly the author hastens to contradict himself. Thus he gives the primary divisions of the Prosimiae as Lamuriformes and Lorisiformes in the text but as Lemuroidea and Tarsioidea in the accompanying diagram. Anthropomorpha comprise Platyrrhini and Catarrhini in the text but tailless apes and men in the diagram. The Anthropoidea are regarded as a suborder but are diagrammed as diphyletic. "The Hominidae consists of a single genus," yet several genera are named and treated. Members of "a single super-genus Pithecanthropus" are named as genera yet are said to show "at most, subspecific differences." Within 5 lines we read "Sub-Families" and "subfamilies." *Gorilla gorilla* is called a subspecies. Zoological Nomenclature is purported but the Rules are repeatedly flouted. Modern concepts of

genetics are presented in one place but in another it is
stated that kinky hair is the only human character that
can certainly be attributed to mutation. "The prefer-
ence of dark Negro males for lighter females . . . oper-
ates to maintain the darkness of the Negro skin." "It
is probable that black skin is such an adaptive character,"
but "there is, however, no evidence that in this particular
respect, such a differential action of natural selection
ever occurred in the development of man." Such
vagaries of thought inspire little confidence in the au-
thor's central view regarding the mental equivalence of
human races.

A critical reader of this book is constantly struck not
only by inconsistencies but also by the selective use of
evidence. Contrary data and contrary expectations on
biological grounds are shunned. Cranial capacity is
cited as evidence to support the amazing statement that
the brain of Neanderthal man "was probably not less
well endowed than that of modern man," but later, in
dealing with modern races, it is claimed that not a trace
of evidence confirms the idea that brain size and intelli-
gence are correlated in man. The author seems to favor
the early evolution of the human brain in its full glory,
yet he writes elsewhere that "the notion that a more
primitive type simply produced, by spontaneous genera-
tion as it were, a more advanced type . . . no longer
agrees with the facts." Indications that some cultural
traits have a genetic basis are "written off" because the
possible effects of the environment were not wholly elimi-
nated, but evidence for environmental effects are accepted
without regard to possible genetic factors. Associations
are outlawed as causes when genetic factors are involved,
but are accepted for environmental effects.

The section on the classification of primates, though
charged with contradictions and other evidences of hasty
preparations, contains one highly commendable feature.
This is the diagram that brackets the subgroups into dif-
ferent and often overlapping combinations. The same

scheme I have found to be very effective in bringing together classifications of vertebrates and of fishes, made from different viewpoints.

The evolution of man is rather well epitomized as "a great radiation of human types to a very large extent brought about by mutation, and the operation of other important factors, such as sexual and natural selection, isolation, migration, and the more or less continuous intermixture of many of the types thus evolved to produce new ones." Hybridization is emphasized as a major evolutionary factor, but strangely, as one of distinctively human application. Recent ideas regarding reticulate speciation in plants and animals have not penetrated. Similarly, in criticizing race classifications it is held that "human groups are not static units but dynamic aggregates"—but so also are many if not most races of plants and animals. Quite contrary to sound speciational philosophy is the statement that in tracing human evolution it is necessary to disregard all characters that are subject to environmental effects, mutation or adaptation.

In line with his obvious intent to devaluate races, the author emphasizes ideas of genes and gene frequencies as a modern substitute for the concept of racial inheritance and evolution. Competition, selection and evolution of populations as units appear to lie beyond his evolutionary thought.

Montagu sets up an incomplete definition of race as "a group of individuals or populations with the same or similar characters, which have been determined by heredity" and then fells the race concept by pointing out that this definition not only leads to the recognition of "a red-headed race, a color-blind race and a deaf-mute race," but also fails to delimit races from species and genera. In so doing he either is guilty of a literary foul or is displaying a lack of understanding of the basic concepts of speciation.

One conclusion that many will reach on reading this book is that a sound evolutionary training, with emphasis

on the speciation, is essential to an adequate understanding of the evolution of man.

NOTICES OF NEW BOOKS

The Dinosaur Book The Ruling Reptiles and Their Relatives. By EDWIN H. COLBERT. New York: American Museum of Natural History. Man and Nature Publications, Handbook 14. 1945: 1–156, 92 figs. $2.50.—The story of reptilian evolution is told in rather modernistic style in this handbook. Attention is first attracted by the exclusive lower-case title, which headlines the reptilian group that has caught the public's fancy. Interest is then held by cartoons, by imaginative reconstructions of high merit, by personal-interest pictures and by boldly colored charts. The text, however, is thoroughly authoritative and beneath the sugar coating there is all the information that the public may crave or be able to digest. After ''Introducing the Dinosaurs'' Colbert discusses the ''Pioneer Students of the Dinosaurs'' [and other fossil reptiles] and then enters into an interesting narration on ''Hunting Dinosaurs.'' ''The Age of Reptiles'' is followed by a brief account of the origin and early evolution of the Tetrapoda—good, solid biology. Then the evolution of the reptiles is taken up, with special but by no means exclusive attention to dinosaurs. There is even a brief account of surviving reptiles. Closing chapters deal with the value of paleontology, the distribution of reptilian remains and the method of classifying and naming these fossils. Finally in chart and table there is outlined the stratigraphic distribution and the taxonomy of the important amphibians and reptiles.

Hawaiian Fishes A Handbook of the Fishes Found among the Islands of the Central Pacific Ocean. By SPENCER WILKIE TINKER. Honolulu: Tongg Publishing Co., 1944: 1–404, 506 figs., col. pls. 1–8. $3.50.—Compiled from the treatises on Hawaiian fishes by Jordan and Evermann, Gilbert, Fowler and others, this abundantly illustrated book will prove of much value to any one interested in the rich fish fauna of the Hawaiian Islands. The brief introduction stresses the adaptations of fishes to aquatic existence and their diversity in structure and habits. There are a few words on zoogeographical relationships, in which it is rightly held that the Hawaiian fishes appear to have been

derived from the East Indies, though the unity of the Indo-Pacific fauna is hardly indicated. A few errors are detected, such as the statement that fishes do not hear and that an American anchovy, *Cetengraulis mysticetus*, occurs in Japan. The erroneous inclusion of *Squalus suckleyi* in the Hawaiian fauna is perpetuated and *Seriola dorsalis* is attributed to the fauna on wholly insecure ground. A few species, as *Hymenocephalus tenuis*, are omitted. One of the most remarkable elements in the Hawaiian fauna, the neotenic genus *Scheindleria*, of problematical relationships, is left in *Hemiramphus* where it was uncritically placed by the original describer.

Protozoology. Third Edition. By RICHARD R. KUDO. Springfield, Illinois: Charles C Thomas, 1946: i-xiii, 1–778, figs. 1–336. $8.00.—Considerably expanded and still more abundantly illustrated than the previous editions, this manual of the Protozoa will be extremely useful to students at all levels. The longer part of the book—more than 500 pages—is devoted to a very detailed systematic treatment of the phylum, with biological as well as morphological data. As thus treated the size and diversity of the group is very impressive. The initial, topic chapters include a general introduction to and history of parasitology. Protozoa are then discussed from the viewpoints of ecology; morphology, with emphasis on cytology; physiology; reproduction, with details on mitosis; variation and heredity, with discussions of physiological strains, ''Dauermodifikationen,'' mating types and other points of very general biological concern; major groups and phylogeny. A final chapter, preceding a long index, deals with the collection, cultivation and observation of Protozoa. The text is well written and highly authoritative.

SHORTER ARTICLES AND DISCUSSION

THE RESULTS OF SELECTION AGAINST EXPRESSION OF THE "SHORT UPPER BEAK" MUTATION IN FOWL

SOME years ago we described a recessive mutation in fowl which is characterized by a shortening of the upper beak, a shortening of the long bones of the extremities and death of the majority of embryos toward the end of the incubation period (Landauer, 1941). The degree of shortening of the beak varied within wide limits. The long bones of the legs were more affected than those of the wings and, especially in the legs, the more distal bones were involved to a greater extent than the more proximal ones.

There is no indication that the mutation under discussion increases embryonic mortality prior to the eighteenth day of development. Out of those "short upper beak" embryos of our original material which survived the eighteenth day 13.3 ± 2.0 per cent. hatched. Accordingly, the mutation was referred to as semi-lethal. The propriety of this designation is, however, doubtful. The rate of survival of homozygous "short upper beak" embryos was not uniform in the various *inter se* matings of heterozygous animals (Landauer, 1941, Table 5). For instance, in one mating (31–1939) 20.8 ± 5.8 per cent. of the abnormal animals hatched, whereas in another mating (24–1940) the frequency of hatched "short upper beak" chicks was only 2.2 ± 2.1 per cent. The difference between these two frequencies amounts to 18.6 ± 6.2 per cent. and is significant. On the basis of subsequent experience it must be assumed that in the absence of all modifying genes the "short upper beak" mutation is completely lethal, and that the matings which furnished the basis of our first report varied in regard to the concentration of modifiers.

Realizing that genetic modifiers played a role in deciding between death and survival of the homozygous "short upper beak" embryos, we set out to select for high viability. A second criterion of selection was the degree of abnormality of the upper beak. The results of these experiments are to be reported below.

All our breeding stock for the present experiments consisted of animals which were homozygous for the "short upper beak" mutation. All chicks which hatched in the early matings had a shortened upper beak and in part of them the upper beak was

TABLE 1

INCUBATION DATA FROM *Inter Se* MATINGS OF CHICKENS HOMOZYGOUS FOR
THE "SHORT UPPER BEAK" MUTATION

Year	Number of fertile eggs	Mortality during incubation days in per cent.			Hatched per cent.
		1–6	7–17	18–22	
1941	74	1.4	8.1	51.4	39.2
1942	264	6.8	6.0	44.4	42.8
1943	461	5.2	4.6	41.9	48.4
1944	726	9.9	11.3	25.6	53.2
1945	344	2.9	3.8	16.3	77.0

crossed to one side.   In some of the chicks which, at hatching
time, had only a slightly shortened upper beak the abnormality
gradually disappeared during growth and the beak became en-
tirely normal.   Preference was given to such animals in choosing
the progenitors of the next generation.   From 1943 onward there
appeared an increasing percentage of chicks which, though homo-
zygous for the "short upper beak" mutation, had normal beaks
from the beginning.   Such animals were given preference in
subsequent breeding.

This combined selection toward higher hatchability and de-
creasing abnormality of the beak produced the results shown in
Tables 1 and 2.   Selection had no discernible effect on embryo
mortality during the first seventeen days of development.   No
such result was to be expected, since the lethal effect of the muta-
tion occurs only shortly before the end of incubation.   During
this last period of development, *i.e.*, between the eighteenth and
twenty-second day, mortality dropped under the influence of

TABLE 2

DATA ON FREQUENCY OF OCCURRENCE OF A NORMAL BEAK AMONG EMBRYOS WHICH
DIED TOWARD THE END OF INCUBATION AND AMONG HATCHED CHICKS ; CHICK
MORTALITY DURING THE FIRST TWO MONTHS OF LIFE ; AND FREQUENCY
OF REPAIR OF BEAK ABNORMALITY AFTER HATCHING.   ALL DATA
FROM HOMOZYGOUS "SHORT UPPER BEAK" STOCK

Year	Died 18–22 days of incubation		Hatched			Chicks with a short upper or cross-beak at hatching which survived for two months or more	
	Number	Per cent. normal	Number	Per cent. normal	Per cent. mortality during first two months	Number	Beak became normal in per cent.
1941	38	0	36	0	13.9	36	30.6
1942	117	0	113	11.5	35.7	76	64.5
1943	193	6.2	223	13.5	4.9	125	69.6
1944	186	12.4	386	42.2	4.8	147	60.5
1945	56	35.7	265	70.9	*	*	*

* No complete progenies raised ; hence, no comparable data available.

selection from an initial 51.4 per cent. in 1941 to 16.3 per cent. in 1945.   Chiefly as a result of this reduced mortality during the last few days of incubation hatchability improved during the same period from 39.2 per cent. to 77.0 per cent. (Table 1).

The effect of selection on abnormality of the beak can be demonstrated in several ways (Table 2).   To start with, the frequency of newly hatched chicks with an entirely normal beak rose from zero in 1941 to 70.9 per cent. in 1945.   The degree of shortening of the upper beak, among those newly hatched chicks which showed any deviation from normal, declined steadily until the abnormality had become nearly imperceptible in the majority of cases.   From 1942 onward the beak became gradually entirely normal in 60 to 70 per cent. of those chicks which had shown some beak abnormality at hatching time, and which had survived for at least two months.   Such a repair of the congenital abnormality had been a rare occurrence in the foundation stock.

In our original material a high percentage of the chicks died during the first two months of life.   This mortality was undoubtedly brought about by inanition on account of severe beak abnormalities and constitutes natural selection against the extreme degrees of expression of the mutation.   With disappearance of the more severe beak defects chick mortality declined to about the level of other stocks.

Among the embryos which died between 18 and 22 days of incubation none with normal beaks were found during the first two years of selection, but from 1943 to 1945 the incidence of late embryos without beak abnormality rose from 6.2 per cent. to 35.7 per cent.   It is important to note that among the embryos which died prior to hatching, with one exception, every individual mating in these experiments gave rise to at least one specimen with an abnormal beak.   The single exception was a female in our 1945 matings which produced only five survivors of the eighteenth day of development, all normal.   It is unlikely, therefore, that reverse mutation had occurred during the period of selection.

In the later generations of our experiments a few individuals were observed which had at maturity an upper beak that was *longer* than normal.   In some of these cases the upper beak had been normal at hatching and became too long subsequently; the remainder had a somewhat shortened upper beak at hatching time, the upper beak gradually becoming normal and finally excessive in length.   These cases are of considerable interest.   They

indicate that the modifying genes do more than suppress the effect of the ''short upper beak'' mutation; these genes play an active role in promoting growth of the upper beak.

It was mentioned earlier that one of the features of the ''short upper beak'' mutation is a shortening of the long bones, especially those of the legs.   This abnormality became less pronounced in our stock *pari passu* with the lessening effect of the mutation on beak development.   This may be taken as evidence for the conclusion that the genetic syndrome, as it was found originally, represents a developmental entity.   The physiological mechanism of the mutation, unfortunately, remains unknown.

The ''short upper beak'' mutation was originally found in stock of Houdan fowl.   There is some evidence indicating that the effect which this mutation has on long bone length is not entirely recessive or, at any rate, was not so in the original stock.   It seems likely that the efforts of Houdan breeders to shorten the extremities of their animals led to unmasking of the lethal by removal of modifiers.   It was only after the original stock had been outcrossed to White Leghorns that the effect of modifiers made its appearance.   The ''short upper beak'' mutation itself has never been recorded in White Leghorn stock.   Yet, when this mutation is transferred to the White Leghorn genotype the ''modifiers,'' in some instances at least, overshoot the mark and give rise to an upper beak which is too long.   This we consider fair evidence for the conclusion that the ''modifiers'' of the ''short upper beak'' mutation are a part of the normal gene complex for beak formation in White Leghorn fowl.

Summary

Breeding experiments in which selection was exercised against the lethal action of and the production of beak defects by the ''short upper beak'' mutation of fowl yielded the following results.   The percentage of hatched chicks became nearly normal. In the final progeny the great majority of chicks had a normal beak at hatching time, and most of those chicks which at first had a slight shortening of the upper beak became normal during growth.   In some instances the upper beak at maturity was longer than normal.

The effect of the ''short upper beak'' mutation on long bone length became lessened under the influence of selection against lethal action and beak deformity.

The "short upper beak" mutation was found in Houdan stock. The modifiers of this mutation were picked up after outcrosses to White Leghorn fowl.   It is concluded that the "modifiers" are part of the normal genic make-up of beak development in the White Leghorn breed.

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NOTES ON GRAPHIC BIOMETRIC COMPARISONS OF SAMPLES

THE recent note by Simpson (1945) and that of Hubbs and Perlmutter (1942), both in this journal, prompt me to record some suggestions which have developed from my experience with the graphic methods introduced by the University of Michigan workers.   The general purpose or objective of the methods is admirable, *i.e.*, the use of diagrams which permit "quick graphic judgment" and which give "some idea of population overlap," as Simpson puts it.   A trend in successive populations can also be shown, even though any two in the succession may not differ significantly from each other.   Many beginners and perhaps others may find, however, that the details of the methods are a serious obstacle to the achievement of those valid aims.   Furthermore, in some cases the methods may run into absurd consequences.

In applying the methods to such a measure as the weight of the spleen or thyroid glands of a large number (*e.g.*, 200) of populations, each of about 15 to 100 individuals, one first labors through the determinations of mean, standard deviation, and standard error of the mean for each population.   Thereafter, in plotting and drawing the lines and rectangles, one finds further difficulties especially in the "inking" process where one is likely to make a messy job of it.   But granting that effort may finally overcome these obstacles, one sometimes finds that the range of the population, as calculated from $M \pm 3\sigma$, extends below zero (see Boyd, 1935).   To me, this outcome and these obstacles were discouraging; in order to attain the ideals indicated above, the following "modification" has been adopted.

Instead of using means, standard deviations, etc., I have followed Boyd in making a percentile analysis of the distribution. This procedure is equally adaptable to normal and highly skewed distributions, and it has the additional merit of rapid use without recourse to machine calculators.   For small populations one will usually find that the median and the quartiles are the only points worth determining; for large populations, any amount of further subdivision is possible.

In representing the percentile analysis graphically, but without complexities of "inking," one may give the range (actual)
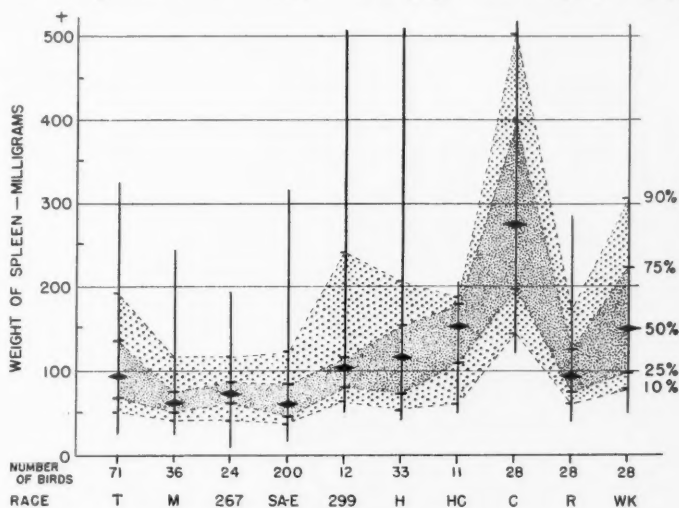

Fig. 1. Graphic percentile analysis of distributions of spleen weights in healthy male pigeons of ten distinct races, arranged from left to right in ascending order of body weight (data from files of Dr. Oscar Riddle).

as a line, the median as an arrow head or diamond, the quartiles as cross-bars, and the deciles (upper and lower) by bars not crossing the line.   To complete the story, the number of individuals making up the population is given at one end of the line. Any reader interested in the significance of difference between medians of two populations can readily obtain the probable errors by the simple formula

$$\text{P.E.} = \frac{\text{Average quartile deviation from median}}{\sqrt{\text{number of individuals in population}}}$$

Or, if more ambitious, he may determine χ^2 values for the original distributions.   As noted previously, however, adjacent populations may not show any significant difference and yet fit into a trend.

One further suggestion may be added.   When a series of populations is arranged for comparison the corresponding points may be connected by lines, as in a graph, and the enclosed areas may be shaded as shown in Fig. 1.   It should be evident that here only one of the populations is large enough to merit an exacting analysis, yet the composite effect is informative.

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